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latifolia (R.Br.) Griseb. and *Calamagrostis*
canadensis (Michx.) Beauv. in relation to
their colonization potential in disturbed
areas, Tuktoyaktuk region, N.W.T.

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ECOLOGICAL STUDIES OF *ARCTAGROSTIS*
LATIFOLIA (R.BR.) GRISEB. AND *CALAMAGROSTIS*
CANADENSIS (MICHX.) BEAUV. IN RELATION
TO THEIR COLONIZATION POTENTIAL IN
DISTURBED AREAS, TUKTOYAKTUK
REGION, N.W.T.

by



WALTER E. YOUNKIN

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
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OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BOTANY

EDMONTON, ALBERTA
FALL, 1974



THE UNIVERSITY OF ALBERTA
FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Ecological studies of *Arctagrostis latifolia* (R.Br.) Griseb. and *Calamagrostis canadensis* (Michx.) Beauv. in relation to their colonization potential in disturbed areas, Tuktoyaktuk region, N.W.T." submitted by Walter Younkin in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

ABSTRACT

A comparative study was made of the ecology of *Arctagrostis latifolia* (R. Br.) Griseb. and *Calamagrostis canadensis* (Michx.) Beauv. to determine the factors influencing their distribution and importance in disturbed and undisturbed tundra communities on the Tuktoyaktuk Peninsula, N.W.T.

Both species are relatively minor components of undisturbed communities, seldom making up more than 2% ground cover. *Calamagrostis*, a species with a wide N/S range, is found in moderately well to poorly drained habitats having either shallowly or deeply thawed soils, while *Arctagrostis*, a species restricted to north of 55°, is generally found in imperfectly drained habitats having relatively deep active layers. Disturbance, such as the removal of the surficial organic mat, results in large increases in their growth and vigor. Cover importance increases 7 to 70 times, plant heights 60 to 160%, seed head production 3 to 5 times and tissue contents of nitrogen and phosphorus 70% and 120% respectively.

The rapid invasion of these grasses into disturbed areas is a function of their small but highly viable and easily germinated seed supply. Important species in the tundra, such as *Betula nana* ssp. *exilis*, *Carex Bigelowii* and *Eriophorum vaginatum*, produce much more seed, but these are either difficult to germinate or have a

low viability. The seeds of both grasses have germination percentages over 70% at temperatures between 5⁰ and 25⁰C. Once established, the increases in growth and vigor are due to the deeper and warmer active layer within disturbed areas and the species' ability to extract nutrients from cold soils.

The active layer of disturbed soils is 38 to 148% deeper than that of undisturbed soils, and in the upper 10 cm temperatures are 1⁰ to 3⁰C warmer than that of undisturbed hummocks and 5⁰ to 10⁰C warmer than hollows. Disturbed mid slopes have the warmest and deepest soils and also the tallest plants and greatest seed production. Analysis revealed a strong positive correlation between plant height and active layer depth ($r=.92$). A comparison revealed that active layers in disturbed areas have three times the volume and contain 2.5 times the total nitrogen, 2 times the available P and 4 times the available K as those under an equal sized undisturbed area. Field observations of root penetration down to 60 cm and laboratory studies of growth in cold soils suggest that, though limited by a combination of low nutrients and low soil temperature in undisturbed areas, both species are able to extract nutrients from soils cooler than 5⁰C and are able to take advantage of the increase in soil volume and nutrients. Their success in disturbed areas is due to a combination of a mobile and a highly viable seed supply which enables them to rapidly invade disturbed areas and a root system sufficiently tolerant of low soil temperatures to take advantage of a relatively large untapped nutrient supply.

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Chapter I

INTRODUCTION

Objective

Oil exploration in the Canadian Arctic has resulted in the disturbance of several thousand hectares of tundra vegetation. Much of this area is being invaded and recolonized by species of low cover importance in the native tundra. Two important graminoid colonizers are *Calamagrostis canadensis* and *Arctagrostis latifolia* (Hernandez, 1973). The objective of this research was to describe the ecology of these two species with emphasis on factors limiting their success and distribution in the native tundra, and factors that contribute to their success as colonizers.

The ability of a species to invade and become established in a new area is dependent upon a number of factors: Availability of seed, seed viability and germination, seed dispersal patterns, seedling establishment, and growth to maturity including reproduction. To a limited extent all of these factors were studied during the past three years. However, certain aspects were deemed more important to this study than others and have been emphasized. There were three phases in the approach to this problem each with one or more subquestions:

- 1) Measurement and characterization of microenvironments in both disturbed and undisturbed areas to determine: a) what are the environmental differences between disturbed and undisturbed sites and how do these differences relate to slope position?

2) Field studies of *Arctagrostis* and *Calamagrostis* on the Tuktoyaktuk Peninsula to determine: a) what is the distribution and importance of these two species in tundra habitats?; b) how does surface disturbance influence their growth and development?

3) Controlled environment studies of these species to determine:

a) what are the germination characteristics of *Arctagrostis* and *Calamagrostis* under a variety of environmental conditions?; b) what is the influence of cold soils on growth, tissue water potentials, photosynthetic rates and tissue nutrient content of *Arctagrostis* and *Calamagrostis*?

Description of Study Area

Geology and Physiography

The Tuktoyaktuk Peninsula is located on the Arctic Coastal Plain to the east of the mouth of the Mackenzie River. Topography in this area is gently rolling, varying from one of closely spaced hills with steep sides to one of broad hills with more gently rolling slopes. Maximum relief seldom exceeds 45 m (Rampton, 1971). Lakes cover 30 to 50% of the area, the result of either thermokarst or modified by thermokarst activity (Mackay, 1963).

This region was covered by one or more advances of the Laurentide Ice Sheet (Hughes, 1972; Bird, 1967; Mackay, 1963), and much of the area is underlain by fluvially deposited sands and silts of Pleistocene origin. These are capped by windblown sands in the northern part

of the peninsula, and by peat, lacustrine deposits and clayey tills and till-like deposits to the south (Rampton and Mackay, 1971). There is evidence to suggest that the last advance of the ice during the Wisconsin did not reach the northern tip of the peninsula (Mackay, 1963; Hughes, 1972), and that with the retreat of ice there was a postglacial submergence of the entire peninsula with a subsequent uplifting to its present position (Mackay, 1963). However, series of raised beach ridges characteristic of postglacial rebound in the eastern and northern Arctic are lacking.

Permafrost

The Tuktoyaktuk Peninsula lies within the zone of continuous permafrost which, except under deep lakes, extends to depths of 100 to 300 m. Associated frost features are common, their occurrence and extent being governed by soil texture and the hydrologic history of each area (Rampton and Mackay, 1971). Common features include frost hummocks on moderately well drained hilltops and hillsides, polygons in poorly drained lowland sites and pingos apparently arising from former lake bed sites (Mackay, 1963). Much of the permafrost is high in water content and ranges from 50 to 500% of water to soil on a dry weight basis (Rampton and Mackay, 1971). These massive bodies of subsurface ice or icy sediments range from 0.8 to over 6 m in thickness and cover tens of square kilometers. The tops of the ice sometimes coincide with the annual depth of the active layer but more frequently lie at depths of 6 m or more (Mackay, 1963; Rampton and Mackay, 1971). Disturbance of the vegetation and organic matter which insulates them can lead to massive slumping and thermokarst topography.

Climate

The Tuktoyaktuk region lies north of the Arctic Circle, and is geographically considered part of the Arctic. However, both climatologically and biologically there are differences of opinion as to what constitutes the true boundaries of the Arctic. Hare and Ritchie (1972) have suggested the tree line as a significant climatic boundary, citing net radiation and vegetation structure as the key interlocking factors influencing climate. Bryson (1966) presents evidence that climatic regions in Canada are a function of air mass frequency, the southern edge of the arctic tundra coinciding with the mean position of the Arctic front in summer. Others have suggested the Nordenskjold line relating the mean temperatures of both the warmest and coldest months, the 10°C isotherm for the warmest month or a line 80 km north of the northern limits of coniferous trees (Polunin, 1951). By all definitions the Tuktoyaktuk Peninsula is considered part of the Arctic, although only marginally so (Mackay, 1963), being only approximately 115 to 160 km north of the coniferous tree line with both the Nordenskjold line and 10°C isotherm passing just across the base of the peninsula (Thompson, 1967).

In the Arctic the concept of four seasons so familiar to those living in temperate areas is not easily applied. The vernal equinox may occur in March but spring thaw and the beginning of the growing season come in late May to early June with fall coloration occurring by late August or early September (Thompson, 1967). For this reason the climate discussion will be broken into winter and summer.

During the eight months or more of winter, sun angles are low and days are short and for nearly three months there is continuous darkness. High pressure areas cover all of northern Canada resulting in relatively stable weather conditions and a climate, even in coastal areas, that is continental in character (Mackay, 1970). On the Tuktoyaktuk Peninsula mean temperatures from October through May range from -5°C to -30°C (AES, 1972). Snowfall is relatively light, the air being too cold to permit formation of snow-producing clouds. The yearly average snowfall is less than 60 cm with the largest snowfalls usually occurring in October (AES, 1972). Winds are surprisingly light during the winter months generally coming from the northwest at speeds of less than 16 km/h (Thompson, 1967).

Following the first sunrise in February, the days gradually lengthen until May when daylength becomes continuous for nearly three months. By the end of May, temperatures rise above freezing for long periods of time and the snow begins to melt rapidly. The ice breakup on Tuktoyaktuk harbor begins by mid June, and by the end of June it and most of the surrounding lakes are ice free (Mackay, 1963).

During the summer months the Arctic Front moves over the northern boundary of the boreal forest and the oceanic character of the Tuktoyaktuk Peninsula becomes more apparent. The weather during these months is unstable; freezing rains and snow can occur at any time and coastal fogs are common when the winds blow inland. Storms often accompany or follow fog banks with winds which can reach 80 to 115 km/h (Mackay, 1963).

Of the 12 cm or less of yearly precipitation, 60% falls as rain and most of that during July and August (AES, 1972). Ameliorated by the proximity to the ocean, summer mean daily temperatures range from 4 to 10°C compared with 10 to 13°C for Inuvik only 160 km further inland (Table 1). Summer maxima of 25 to 30°C, though not frequent, are common, generally occurring when the winds are blowing from the south or southwest bringing warm air from the interior.

Table 1. Monthly and yearly means of temperature and precipitation over a 14 year period at Tuktoyaktuk, N.W.T. (69° 27'N 133° 00' W).

Climatic Factors	May	June	July	August	Sept.	Year
Mean Daily Temperature (°C)	-4.6	4.6	10.3	8.7	2.2	-10.7
Mean Daily Maximum Temperature	-1.1	9.1	14.9	12.2	4.6	- 7.2
Mean Daily Minimum Temperature	-8.2	0	5.8	5.2	0	-14.2
Number of Days with Frost	30	16	1	1	17	277
Mean Total Precipitation (cm)	.7	1.3	2.2	2.8	1.4	12.7

Soils

Tedrow and his associates (Tedrow, 1966; Tedrow and Harries, 1960; Tedrow and Cantlon, 1959) have contributed greatly to the identification of arctic soils and to the clarification of the soil forming processes occurring in arctic regions. Janz (1974) has suggested that soils of the Tuktoyaktuk Peninsula and adjacent regions have developed in reponse to variations in soil moisture influenced by topography and permafrost. He has identified four soils at the Sub-Group level based on the revised Canadian soil classification system (Day and Lajoie, 1974); Mesic Organo Cryosols occurring in wet lowland areas, Regosolic Static Cryosols associated with beach sands and receding lake margins,

Gleysolic Static Cryosols in poorly drained areas often associated with alder, cotton grass and sedge heath vegetation and Gleysolic and Regosolic Turbic Cryosols occurring on imperfectly drained hilltops and hillsides associated with birch and willow heaths. Haag (1972) provides a detailed profile description of a typical Gleysolic Turbic Cryosol developed under a dwarf shrub heath community near Tuktoyaktuk.

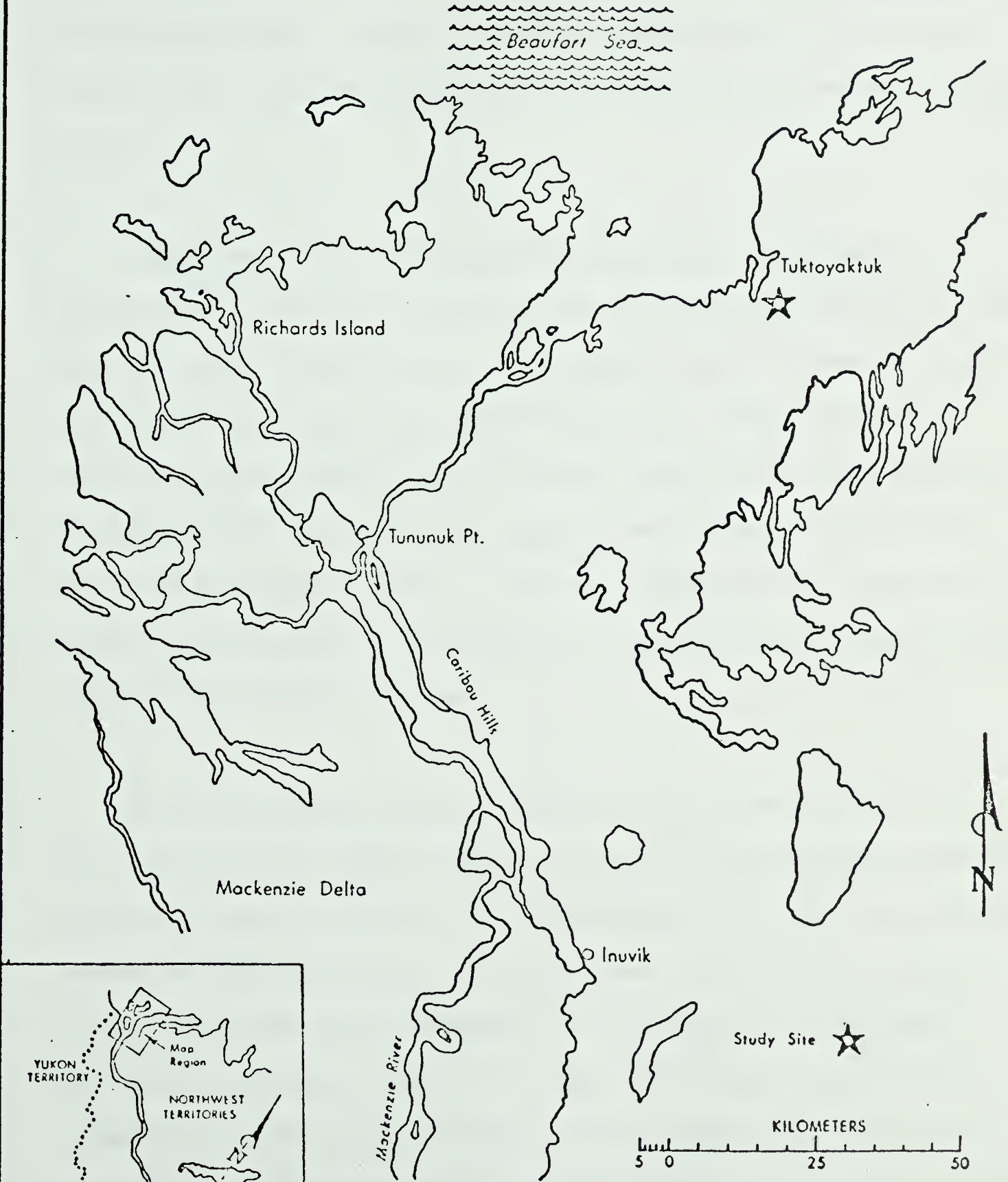
Vegetation

The Tuktoyaktuk Peninsula is covered by a low shrub-heath tundra characteristic of many low arctic regions in contrast to the polar desert or polar semi-desert of the High Arctic. Corns (1974) studying the vegetation of the peninsular area classified it according to species composition and drainage into 5 major types with an estimate of the area covered by each: low shrub-heath found on well-drained hilltops and slopes, 69%; herb-low shrub-heath characterized by an increase of sedges and found on moderately drained flat to very gently sloping areas, 23%; medium shrub-heath occupying imperfectly drained mid slope positions and characterized by the occurrence of *Alnus*, 4%; and tall shrub-herb type restricted to lakeshores and stream banks, 1%.

Intensive Study Site

The intensive study site (69° 27'N 133° 00'W), Camp Waltrus, is located 10 km south of the village of Tuktoyaktuk on a 1965 seismic line (Fig. 1). The portion of the line and surrounding tundra studied is on a hill with an 8 to 10% slope to the northeast. The disturbed part of the study area was bladed in the summer of 1965; this resulted

FIG.1 Study Area



in the removal of all vegetation and rootstocks and most of the active layer. The remaining material is a sandy clay loam. Measurements made across the seismic line using undisturbed hummocks as a baseline, indicate that the surface of the seismic line is 50 to 70 cm below the adjacent tundra surface. Of this, approximately 30 to 45 cm was pushed aside during the blading and the remainder subsided due to permafrost meltout.

Vegetation in the undisturbed tundra provides essentially 100% ground cover. The top and sides of the hill are characterized by *Betula nana* ssp. *exilis*, *Salix glauca*, *Ledum palustre* ssp. *decumbens*, *Vaccinium vitis-idaea* ssp. *minus* and *Empetrum nigrum* ssp. *hermaphroditum* and the bottom of the hill by *Carex Bigelowii*, heaths and widely scattered shrubs of *Betula nana* and *Salix glauca*. The vegetation cover in the disturbed area ranges from 30 to 40% and is dominated by *Arctagrostis latifolia* and *Calamagrostis canadensis*. Taxonomy follows that of Hulten (1968) unless otherwise stated.

For the purpose of the investigation the hill was divided into top, mid and bottom slope sections with 5 x 15 m representative stands selected from each section in both the disturbed and adjacent undisturbed tundra for intensive study. For convenience each stand was assigned a code number made up of a letter (D = disturbed, N = undisturbed) and number (1 = top, 2 = mid, 3 = bottom) indicating slope position. In addition, within all undisturbed stands a common frost feature was the occurrence of numerous small mounds (hummocks) .5 to .75 m in diameter separated by hollows 15 to 25 cm deep. These hummocks and hollows were recognized as having distinct microenvironments and vegetation and

were treated separately in taking any measurements.

Chapter II

TAXONOMY AND RANGE

Both *Arctagrostis* Griseb. and *Calamagrostis* Adans., are restricted to cool or temperate regions and contain species which are circumpolar in distribution. *Arctagrostis* is a more truly northern genus, having no species occurring below 50°N (Klebesadel, 1969) while *Calamagrostis* has species occurring in both hemispheres (Gould, 1968) with those in the northern hemisphere being found as far south as 22°N (Hitchcock, 1950).

Arctagrostis

Arctagrostis is a genus of little taxonomic differentiation, and though 17 species have been described at one time or another (Tolmachev, 1964), only 2 to 3 are recognized on a world-wide basis. Hulten (1968) recognizes two species: 1) *Arctagrostis latifolia* (R.Br.) Griseb. which is circumpolar and contains three varieties; *Arctagrostis latifolia* var. *latifolia*, the more northern circumpolar form and the subject of this report, *A. latifolia* var. *arundinacea* (Trin.) Griseb. and *A. latifolia* var. *angustifolia* (Nash) Hult. The latter two are taller and extend the range of the species to its southern limits. 2) *A. poaeoides* Nash, a species of doubtful distinction from *A. latifolia* with a range restricted to central Alaska. Tolmachev (1964) recognized *Arctagrostis latifolia* but considered it to be only weakly differentiated throughout its range and containing at best only two subspecies, the type subspecies and *A. latifolia* ssp. *gigantea* (Turez ex Griseb.) Tzvel. occurring in the mountain ranges of eastern Siberia. However, he raised

Hulten's *A. latifolia* var. *arundinacea* to full specific rank and demoted *A. poaeoides* to a subspecies of *A. arundinacea*. For the purposes of this report the taxonomic treatment of Hulten will be followed.

Arctagrostis latifolia var. *latifolia* is a relatively tall perennial grass found almost entirely in arctic regions. Its range is circumpolar and in the western hemisphere extends from approximately 60°N to about 80°N on Ellesmere Island (Fig. 1) (Hulten, 1962). In the U.S.S.R. this range is extended southward to 50°N along mountain ranges of eastern Siberia and, though not common, has been reported as far south as 54°N in the Canadian Rocky Mountains (Hrapko, 1970). The species tolerates a wide range of tundra conditions and is found as a common but unimportant member of many tundra communities (Tolmachev, 1964). It ranges in height from 20 to 50 cm in the arctic islands (Porsild, 1957) to over 100 cm in the Tuktoyaktuk Peninsula. It has broad leaves 0.5 to 1 cm in width and generally stout culms, spreading by means of stout branching rhizomes.

Calamagrostis

In comparison to *Arctagrostis*, the genus *Calamagrostis* is widely differentiated, containing over 100 species (Tolmachev, 1964) which occupy a wide range of habitats over much of the northern hemisphere. The majority of these species are restricted to temperate or boreal regions, only 10 being found in the Arctic. Of these, *Calamagrostis canadensis* (Michx.) Beauv. is probably one of the more important, occupying extensive areas in southern and southcentral Alaska which are used

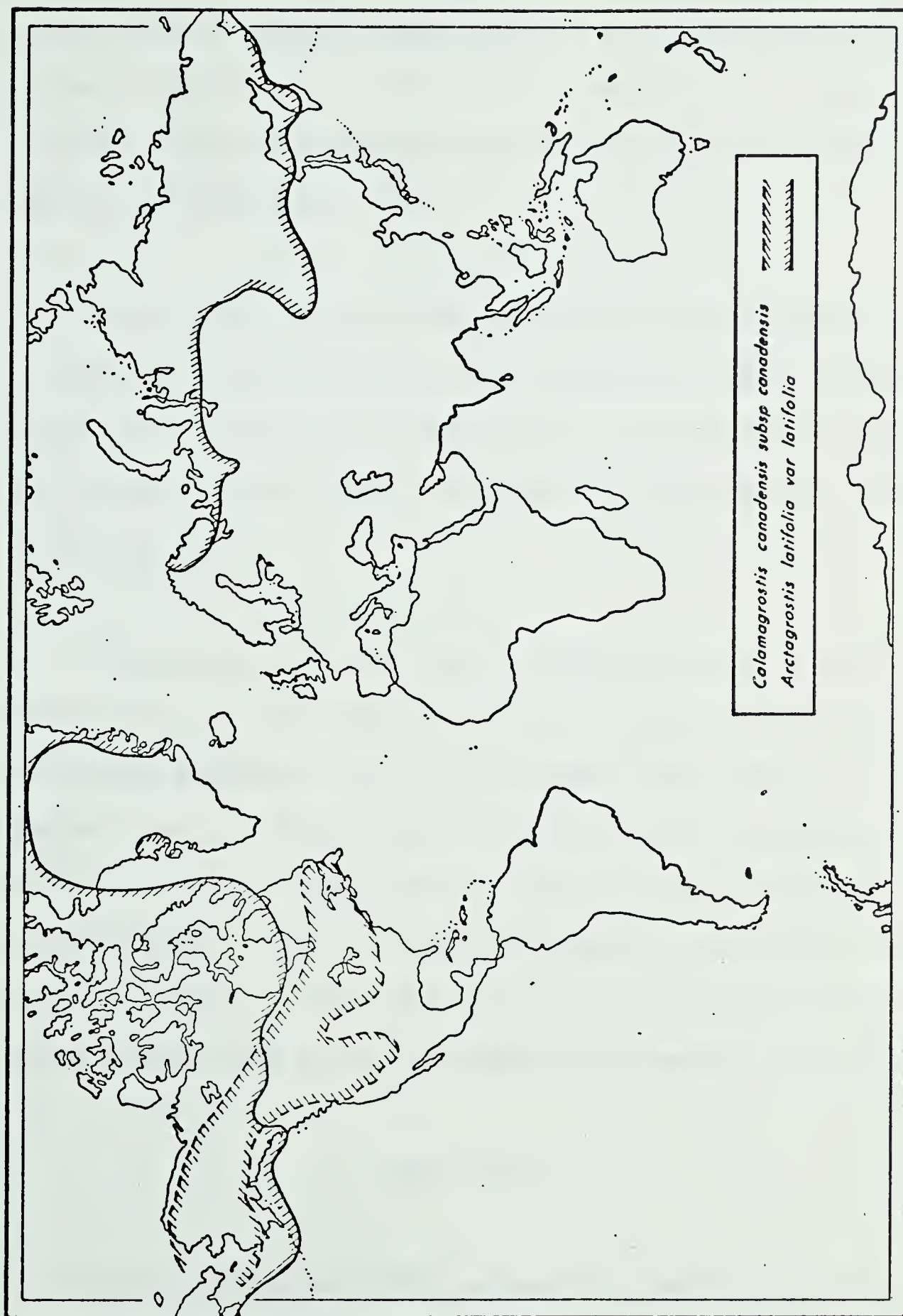


Figure 2 . Distribution of *Arctagrostis latifolia* var *latifolia* and *Calamagrostis canadensis subsp canadensis*.
After Hulten (1962)

for forage (Mitchell and Evans, 1966) and in boreal and arctic regions of western Canada where it invades after fire or logging, thus aiding erosion control. Nygren (1954) considers this to be the most successful of the New World species and relates its success to its production of sexual, semi-apomictic and obligate apomictic strains which reinforce the species' plasticity.

Hulten (1968) recognizes two subspecies of *Calamagrostis canadensis*; *C. canadensis* subsp. *canadensis* and *C. canadensis* subsp. *Langsdorffii* (Link) Hult. Both have arctic and boreal distributions in North America, but the latter is more nearly circumboreal, also occurring in Asia and Siberia.

Calamagrostis canadensis subsp. *canadensis* is restricted to North America but has a wide north-south range extending from near 35°N in the Arizona mountains to 69° at Tuktoyaktuk, N.W.T. (Fig. 2). The species appears to have a large ecological amplitude occurring in a variety of habitats ranging from lowland wet sites to windswept alpine ridges (Mitchell, 1968). In general morphology this species is similar to *Arctagrostis latifolia* and at times is easily confused with it, having culms up to 1 m tall and leaves 3 to 8 mm wide (Hulten, 1968).

Past History

According to Hulten (1937) *Arctagrostis latifolia* is a truly circumpolar Arctic-montane species which is believed to have spread from the mountains of northeast Asia to North America before the last glaciation. It did not reach the southern rim of the ice but was trapped to the

north of the ice in refugia where its spreading capacity was contained and its ecological amplitude reduced by the isolation and selection pressure imposed by the glacial period.

Calamagrostis canadensis is believed to have arisen from members of the circumboreal flora (Hulten, 1937). These species, partially due to their intolerance to cold, did not reach the northern limits of the ice but were contained in large refugia and involutions within the ice sheet far south of its northern extension. Here they were not as genetically isolated and through interbreeding and recombinations retained their spreading ability and ecological amplitude. Today most of the widespread plants of the arctic and boreal belts belong to this latter relatively broadly adapted group.

Chapter III

OCCURRENCE AND IMPORTANCE IN TUNDRA HABITATS

Arctagrostis latifolia and *Calamagrostis canadensis* are seldom important cover species in undisturbed tundra vegetation, and little is known about their habitat preference aside from their inclusion in species lists in various vegetation studies. In a review on the vegetation studies of arctic Alaska (Britton, 1966), *A. latifolia* was listed as a minor component of a number of plant communities, including dry meadows on the lower slopes of the Brooks Range, dwarf shrub heath covered hillsides in the foothills and raised beach ridges on the coastal plains. Dennis (1969), working on the coastal plain near Barrow, Alaska reported that *A. latifolia* was an important component of communities on raised beach ridges and observed that in whatever habitat it was found, it generally occupied the better drained positions. He found no significant or consistent correlation between the cover importance of this species and a number of measured environmental parameters, including active layer depth, bulk density, soil moisture and soil temperature. In arctic U.S.S.R., Tolmachev (1964) described *A. latifolia* as a species occupying a wide range of habitats from the edges of low boggy areas to sandy terraces. It appears to be most important in those areas having accumulations of fine mineral soil, moderate drainage, and relatively deep winter snow cover. Corns (1974) in an investigation of plant communities in the Tuktoyaktuk region, N.W.T., found both *A. latifolia* and *C. canadensis* as common, but minor components of imperfectly to moderately well drained communities, but absent in those which were very wet. Hernandez (1973) in a study of disturbed communities in

the same region identified both species as important colonizers in disturbed upland tundra.

The objective of the studies described in this chapter was to determine the relative importance of *Arctagrostis* and *Calamagrostis* and other colonizers including *Poa lanata*, *Festuca brachyphylla*, *Senecio congestus*, and *Epilobium angustifolium* (Hernandez, 1973) in undisturbed habitats and the magnitude of their change in importance with disturbance.

Undisturbed Tundra

Methods

The study was begun in mid-August, 1972 when both grass species were in flower. Stands, based upon a uniformity in physiognomy and pattern of dominant species, were selected randomly but in such a manner as to include a variety of habitats and associated communities, often working on a moisture gradient from lowlands to uplands. Each stand was placed into topographic and soil drainage classes according to the Canadian Department of Agriculture Soil Classification System (1970). Dominant species were identified in each layer of the vegetation and later this information was used to classify the communities into subgroups according to Corns (1974). Within each stand a 5 x 10 m sample area was delimited. Counts were made of vegetative and flowering clumps of selected grass species by pacing back and forth at one metre intervals, (50 cm of sampling line per sample area). Only individuals within 50 cm of the line were counted. Species importance was based upon density (the number of clumps counted per sample area) while vigor was generally based upon the proportion of clumps flowering. It is

recognized that in many cases, clumps were joined by rhizomes and were, therefore, not truly separate individuals. This was not considered important to the purpose of this study. Depth of the active layer was measured with a graduated steel rod at 10 points within the sample area, using hummock centres as the point of measurement in hummocky tundra.

Results

Calamagrostis canadensis, though appearing to be absent in most habitats, is actually more widely dispersed in the tundra than is *Arctagrostis latifolia*. It occurred in all habitats except the wet depressional, reaching its greatest importance in moderately well drained uplands (Table 2). In no habitat, however, was it very vigorous, generally appearing chlorotic with fewer than 5% of the clumps flowering. Because of its non-distinctive, vegetative appearance and the general absence of seed heads, it is easily overlooked.

Arctagrostis latifolia is common in imperfectly to moderately well drained habitats of all topographic positions. It is most important on imperfectly drained areas, decreasing in importance on dry upland or wet lowland sites. It seldom occurs on soils with an active layer depth of less than 35 cm, appearing to favour areas where the mineral soil is only covered by a thin layer of organic matter. Seed head production was greatest on moist to mesic sites. In general, the vigor of this species was good in all areas of occurrence, with 30% of the clumps flowering.

Table 2. Relationship of physical site characteristics to mean number of clumps and number of flowering clumps of selected species.

PHYSICAL SITE CHARACTERISTICS					MEAN NUMBER OF CLUMPS AND NUMBER IN FLOWER PER STAND (50m ²)				
Topographic Class	Soil Drainage Class	Mean Active Layer Depth (cm) (8-15 Aug.)	Community Subgroup	Number of Stands	<i>Arctagrostis latifolia</i> Total Flower	<i>Calamagrostis canadensis</i> Total Flower	<i>Poa lanata</i> Total Flower	<i>Festuca brachyphylla</i> Total Flower	
Depressional	Very Poor	30 ± 2	Sedge	5	0	0	0	0	0
Nearly level	Poor	26 ± 1	Sedge-Cotton- grass-Heath	6	.3	35	0	0	0
	Moderately well drained	27 ± 1	Raised Center Polygon	6	3	9	2	0	0
Very gently sloping	Imperfect	43 ± 3	Alder	3	46	72	.3	1	0
Gently sloping	Imperfect	44 ± 1	Birch-Willow- Heath	5	61	58	0	1	0
Moderately sloping	Moderately well drained	47 ± 2	Birch-Willow- Heath	6	11	59	0	2	1
Strongly sloping	Moderately well drained	49 ± 1	Birch-Heath	4	0	67	0	9	1
Hill top	Moderately well drained	42 ± 1	Birch-Heath	4	0	115	0	4	1

Many of the other less important colonizing species, such as *Epilobium angustifolium* and *Senecio congestus*, were not found in any undisturbed tundra habitats. Of the remaining grasses, *Poa lanata* and *Festuca brachyphylla* were restricted to drier sites where they were of very low density. That they prefer drier sites is also suggested by their greater importance in well drained disturbed areas (see next section).

Disturbed Tundra

In 1970 and 1971 Hernandez (1972) surveyed a number of sites in the Mackenzie Delta region disturbed as a result of oil exploration. The seismic lines constructed in the summer of 1965 were the most severe. All vegetation and soil down to permafrost was bulldozed aside for geophone placement. In almost all cases, rhizomes and root systems were entirely removed so that any revegetation which took place was the result of seeding from the adjacent tundra. Comparisons of composition and cover importance between adjacent disturbed and undisturbed communities provide insights into the habitat preferences of invading species and the relative abilities of different species to invade and establish in undisturbed areas.

Methods

Hernandez (1972) studied eight stands along 1965 seismic lines in the Tuktoyaktuk region. Four of these were in moderately well drained upland, low shrub-heath tundra, two in wet sedge meadows and one in poorly drained cottongrass-low shrub tundra. At each stand, composition and cover of plant communities in both disturbed and adjacent undisturbed tundra were taken. Sampling was done using sixteen 1 m^2 quadrats stratified

randomly located along 30 m transects both within the disturbed and adjacent undisturbed tundra (Hernandez, 1972). Important species from both are listed in Table 3, by community type. Per cent aerial cover, as presented by Hernandez, is shown for those species occurring in the disturbed area. The ratio of cover on undisturbed to disturbed tundra was calculated using Hernandez's (1972) cover values and indicates the magnitude and direction of cover change due to disturbance. This calculation ($\% \text{ cover in disturbed} \div \% \text{ cover in undisturbed}$) results in a value of one for the species in the undisturbed tundra, and some value either larger or smaller for the species in the disturbed tundra. Species in the disturbed tundra, with a value of less than one are considered cover decreaseers; those with a value greater than one are considered cover increaseers.

Results

The 1965 seismic lines running through low shrub-heath communities have four species which are cover increaseers: *Arctagrostis latifolia*, *Calamagrostis canadensis*, *Poa lanata* and *Carex Bigelowii* (Table 3).

All of these except *Carex Bigelowii* are of very low cover value in the undisturbed tundra, generally being less than 0.5%. *Carex Bigelowii* has a cover in the undisturbed tundra which ranges from 0.5 to 3.3%. Of these species, *Arctagrostis latifolia* and *Calamagrostis canadensis* are the most important increaseers, providing the most cover and having the highest cover ratio changes. Species important in the undisturbed tundra, such as *Betula nana* ssp. *exilis* and *Salix glauca* have very low cover values in disturbed areas ranging from 0 to 4%.

TABLE 3. Percent cover in disturbed areas and ratio of cover on undisturbed to adjacent disturbed tundra of species occurring in 1965 summer seismic lines passing through various community types in the Tuktoyaktuk Peninsula.

Species	COMMUNITY TYPES									
	Low Shrub-Heath									
	# 1	# 2	# 3	# 4		Cottongrass	Sedge	Sedge		
	% cover	% cover	% cover	% cover	ratio	Meadow	Meadow	Meadow	ratio	ratio
	ratio	ratio	ratio	ratio	ratio	% cover	% cover	% cover	ratio	ratio
<i>Arctagrostis latifolia</i>	5.6	14.6	7.8	5.7	1:29	1.5	1:7.5	-	-	-
<i>Calamagrostis canadensis</i>	9.5	7.6	6.8	6.6	1:33	-	-	-	-	-
<i>Poa lanata</i>	6.2	2.0	1.3	0.7	1:3.5	-	-	-	-	-
<i>Carex bigelowii</i>	6.6	1.7	2.3	13.0	1:3.7	0	0	-	-	-
<i>Arctophila fulva</i>	-	-	-	-	-	32.5	1:162	8.4	1:42	13.1
<i>Carex aquatilis</i>	-	-	-	-	-	-	3.8	7.6	-	-
<i>Eriophorum vaginatum</i>	-	-	-	-	-	5.4	1:31	-	-	-
<i>Betula nana</i> ssp. <i>exilis</i>	0.5	1:04	0	0	1:-	-	-	-	-	-
<i>Salix glauca</i>	1.0	1:09	0	0.7	1:33	-	-	-	-	-
<i>Lupinus arcticus</i>	0.1	1:03	0	0	1:-	-	-	-	-	-
<i>Vaccinium uliginosum</i>	-	0	0	-	-	-	-	-	-	-
<i>Vaccinium vitis-idaea</i> ssp. <i>minus</i>	0	0	0	0	1:-	0	1:-	-	-	-
<i>Dryas integrifolia</i>	-	-	-	0	1:-	-	-	-	-	-
<i>Rumex arcticus</i>	-	-	-	-	-	0.6	1:3	-	-	-
<i>Bryophytes</i>	2.0	1:09	13.6	1.8	1:06	6.4	1:21	9.2	1:26	5.0
										1:26

* In determining ratios, when cover in undisturbed tundra was expressed as < .5% (Hernandez, 1972) .2% was arbitrarily selected as the divisor.

** In instances where species important in the undisturbed tundra were absent in the disturbed tundra the ratio of change was infinite and is expressed as -.

The remaining disturbed communities are more moist. These sites have fewer species able to establish and are dominated by *Arctophila fulva*, a grass species which is essentially absent in the adjacent undisturbed tundra.

Discussion

Of the two important colonizing grasses, *Calamagrostis canadensis* appears to have the widest ecological amplitude, being able to survive both on shallowly, or deeply thawed soils, and under imperfectly to moderately well drained conditions. It is found on mineral and organic soils, but is more frequently found on peaty soils or in peaty areas between hummocks or frost boils. That this species has such a wide ecological amplitude was not unexpected from the wide extent of its range (Chapter 2). Its lack of vigor, however, (as denoted by its low production of flowering heads) suggests that on the undisturbed tundra at least, conditions are approached that are near its limits of tolerance, and that its continued existence is dependent upon tundra disturbances which provide it with a more suitable habitat for seed production.

Arctagrostis latifolia has a narrower range of tolerance, being most important under imperfectly drained conditions, and being restricted to soils with a seasonal active layer greater than 35 cm. This species is generally not found growing in deep organic soils. It produces seed heads in all areas of occurrence and numerous seed heads in more favourable areas. This, along with its generally vigorous appearance on both disturbed and undisturbed sites, and the limitation of its

range to northern areas, indicates that it is the more highly adapted of the two species to arctic environments.

Species common in the undisturbed tundra such as *Betula nana*, *Salix glauca* and *Eriophorium vaginatum* have little ability to reinvade and colonize disturbed areas. Seed production and dispersal is not a problem for any of these species, and it is probable that seeds from these species virtually shower down on disturbed sites. The species most important in disturbed areas, *Calamagrostis* and *Arctagrostis* on moderately well drained to imperfectly drained sites, and *Arctophila fulva* on wet sites, are nearly non-existent in the native tundra. Though dispersal mechanisms of each of these are probably as good as any of the important native tundra species, the total amounts of seed produced is far lower. This would lead one to speculate that the failure of the important native species to invade disturbed areas lies either in their inability to produce viable or easily germinated seed, or in their inability to establish as seedlings, or both. Considering the low seed supply, the important colonizing species must provide both a highly viable seed supply and have the ability to establish once the seeds germinate.

Chapter IV

MICROENVIRONMENT

During the summers of 1971 and 1972, measurements were made of various microenvironmental factors within the disturbed and adjacent undisturbed areas to determine factors which might influence growth and distribution of the two grasses under investigation. These included air and soil temperature, active layer depth, soil moisture, snow depth and duration, and soil nutrients.

Methods

Air and Soil Temperature

Air and soil temperatures were taken during the summer of 1972 using two nine point Grant Recorders and thermistor probes. The Grant Recorders were set up at hill-top and hill bottom positions. Thermistors taped to wooden stakes at 10 cm intervals were placed to a depth of 30 cm in disturbed areas and undisturbed hummocks and to 20 cm in undisturbed hollows. Air temperature was taken at 15 cm at the undisturbed hill-top position using a shielded and ventilated thermistor. All temperatures were recorded at 1 hr intervals throughout the summer. At two periods during the summer the probes were placed in the mid-slope position to provide information comparable to that from top and bottom slope positions. Daily and weekly means were computed using temperatures averaged over 3 hr intervals. Surface temperature readings in both disturbed and undisturbed areas were taken several times during the summer using a Barnes Engineering radiation thermometer.

Active Layer Depths

Depth of active layer measurements were taken at weekly intervals in 1972 from three permanently marked transects across disturbed and adjacent undisturbed tundra at each slope position. On each transect nine measurements were made using a graduated steel rod; three from marked points within the disturbed area and three each from hummocks and adjacent hollows in the undisturbed tundra. This resulted in a total of 27 measurements per slope position. Measurements were taken using a graduated, 7 mm diameter steel rod.

In addition, during the summer of 1972 a study was undertaken to determine the influence of live vegetation on active layer depth. Ten pairs of hummocks were selected at an undisturbed hill-top position. All of the vegetation within a 45 cm radius was clipped to the soil surface on one hummock of each pair, the other was left undisturbed. At weekly intervals the active layer depth was measured from a permanently marked point on each hummock.

Soil Moisture

Soil moisture samples were taken weekly in 1972 using a 7.5 cm diameter split tube sampler. One sample from 0 to 5 cm and one from 10 to 15 cm was taken from the vicinity of four permanently marked areas within each disturbed site and from two hummock and two hollow locations in each undisturbed site. Soil moisture was determined gravimetrically with drying at 105°C. Soil water potentials were determined from desorption curves based on pressure plate readings at 1/3, 3 and 15 bars.

Snow Depth

Snow depth measurements in disturbed and adjacent undisturbed areas were made twice in early June using the active layer probe. Fifty measurements each were made down the center of the seismic line and 2 m to the side of the seismic line at approximately 1 m intervals.

Soil Nutrients

Nutrient samples were taken from the top 10 cm at two locations within each disturbed site, composited and then frozen until analyzed. Nutrient data for undisturbed tundra were provided by Janz (1973). Nutrient analyses for N, P and K were provided by the Soil and Feed Testing Laboratory in Edmonton, Alberta following the methods of Horwitz (1970). Total nitrogen was determined by the macro Kjeldahl method, available phosphorus by spectrophotometer after extraction with ammonium acetate and available potassium with a flame photometer.

Results

General Weather Pattern

A general picture of weather during the two field seasons was obtained using data from the Dew Line station at Tuktoyaktuk (AES, 1972), about 11 km north of the study site.

The 1971 growing season was early with snow melt before the end of May. Mean daily temperatures were 1.6° and 3.9°C above normal for May and June respectively. July temperatures were near normal (Table 4) while August averaged 2.1°C below normal. Precipitation during

June of 1971 was about 50% of that normally received and was slightly above normal for July and August (Table 4).

The 1972 season was later than normal. This was not due so much to spring temperatures which were 2 to 3°C below normal for May, as to an above normal winter snow accumulation which remained until the second week in June. Though it shortened the growing season slightly, the increased meltwater may have somewhat compensated for a summer which was unusually dry. Precipitation in June was 50% and in July 33% of that normally received (Table 4). August was slightly above normal in both precipitation and temperature.

Table 4. Mean daily temperatures and monthly precipitation totals at Tuktoyaktuk during the 1970 and 1971 summer field seasons compared to seasonal norms.

Climatic Factor	June			July			August		
	1971	1972	Norm	1971	1972	Norm	1971	1972	Norm
Mean Daily Temp (°C)	8.6	4.7	4.7	11.4	11.7	10.3	6.8	10.8	8.7
Total Precipitation (cm)	0.58	0.58	1.3	2.33	0.68	2.20	3.75	3.05	2.8

Air and Soil Temperatures

Air temperatures reached their peak during mid-July and then began a gradual decline (Table 5). Within the vegetation (15 cm) mean air temperature for the month of June was 7.8°C, for July 13.1°C and for August 10.9°C. A comparison of mean weekly air temperatures within (15 cm) and above (120 cm) the plant canopy shows that in the early part of the season, temperatures within the vegetation boundary layer

are significantly warmer. Dennis (1969) found a similar but less pronounced trend at Barrow, Alaska in 1965. At Tuktoyaktuk this difference decreased as the season progressed, possibly due to increased windiness or cloud cover, but does suggest that the early season microenvironment is more favorable than is suggested by weather bureau records. Air temperatures were not taken within the seismic line but it is reasonable to believe that because of their sunken surface condition, a similar increase in air temperature would occur.

Spot readings of surface temperatures in both disturbed and undisturbed sites were taken on a clear and warm (air temperature 15°C) day in mid-July. Mean soil surface temperatures at both top and mid-slope disturbed sites were 25°C while those at the more moist lowland site and the vegetated undisturbed sites were 16°C. The surface temperature of a path worn through the vegetation by less than one season's use was 22°C.

The hourly soil temperature recordings made in 1972 for disturbed and undisturbed top and bottom slope positions are summarized as weekly means (Table 5). These data show that disturbed soils were significantly warmer than undisturbed soils, the differences being most apparent at -10 cm. In general, disturbed soils were 1 to 3°C warmer than those in hummocks and 5 to 10°C warmer than those in hollows. At 20 cm there was little difference between hummock and disturbed soils until early July when disturbed soil temperatures gradually become 2 to 5°C warmer. At 20 cm the soils in the hollows remained essentially frozen most of the season while those in disturbed sites warm to 6 to 10°C. These data suggest that the leveling of hummocky areas is as important as

Table 5. Mean weekly air and soil temperatures in undisturbed and adjacent disturbed areas near Tuktoyaktuk, N.W.T. during the 1972 field season.

		T E M P E R A T U R E (°C)											
		+120 cm			+15 cm			-10 cm			-20 cm		
Date	Dew Line	Air						Hollow			Hollow		
		N1	N3	*N1	*N3	N1	N3	*D1	*D3	N1	N3	D1	D3
June 3 - 7	0.8	5.1		0.1	-1.8	-0.9	-1.7	0.3	-1.3	-1.0	-2.5	-0.8	-2.8
June 8 - 14	8.6	11.9		3.0	1.2	-0.3	-1.1	3.7	1.0	0.6	-1.4	0.1	-2.0
June 15 - 21	5.1	7.5		3.6	1.6	0.0	-1.3	4.4	2.2	1.6	-2.0	1.0	-1.9
June 22 - 30	4.2	7.0		3.5	1.3	0.5	-1.4	4.9	3.6	1.9	-1.8	1.8	2.0
July 1 - 7	8.3	11.4		4.3	4.1	0.3	-0.3	6.2	6.8	2.2	-0.1	2.5	4.8
July 8 - 14	12.6	14.0		6.2	6.1	0.6	1.1	8.1	9.4	3.3	1.0	4.2	7.0
July 15 - 21	14.0	14.0		7.4	7.4	1.3	2.2	10.0	11.7	3.8	2.6	6.3	9.9
July 22 - 31	11.9	13.0		5.8	5.5	1.8	2.0	8.2	8.3	3.1	1.4	4.7	7.2
Aug. 1 - 7	12.3	13.0		6.8	5.8	2.0	2.8	9.1	8.7	4.1	1.7	6.0	7.4
Aug. 8 - 14	9.0	8.7		4.8	4.2	2.9	2.0	7.4	7.2	3.0	1.1	5.2	6.2
Aug. 15 - 19	11.7	10.7		5.2	-	4.2	-	8.0	-	3.4	-	5.1	-

* N1 = undisturbed hilltop, N3 = undisturbed hill bottom, D1 = disturbed hilltop and D3 = disturbed hill bottom.

the removal of the turf in bringing about changes in soil temperature.

Differences in soil temperatures were also related to slope position. During most of the season temperatures were monitored at only top and bottom slope positions. These data show that early season soil temperatures in the hill bottom positions were generally cooler than those at the hill-top position (Table 5). During the first two weeks in June differences ranged from 0.8°C between hollows to nearly 3°C between disturbed sites. These differences gradually decreased and by the second week in July mean temperatures at both positions were comparable. These differences are most likely the result of the slightly greater soil moisture associated with the imperfectly drained hill bottom soils.

Due to a lack of thermistors, data on soil temperatures at the mid-slope position were not gathered until near the end of July. A comparison of daily mean soil temperatures between the three slope positions shows that soils on the mid-slope position were warmer (Table 6). The greatest differences were recorded in the disturbed areas. Soil temperature at the upper and lower slope positions remained at nearly the same level while soils in the mid-slope position averaged 2 to 3°C higher ranging from 7 to 11.5°C . In the undisturbed tundra the influence of slope position was much less evident. The mid-slope soils were only 0.1 to 2.1°C warmer than those at other slope positions. Because of the increased solar energy received by an inclined surface, it is reasonable to believe that the disturbed mid-slope soils were warmer during most of the growing season. It is probable that because this is a northeast-facing slope, other slope positions, particularly southwest-facing, would have even greater temperature differences.

Table 6. Daily mean soil temperatures ($^{\circ}\text{C}$) at 10 cm in disturbed and adjacent undisturbed hummocky tundra at top, mid and bottom slope positions near Tuktoyaktuk, N.W.T. during July and August 1972.

		T E M P E R A T U R E $^{\circ}\text{C}$					
		Hummock			Disturbed		
Date		Top	Mid	Bottom	Top	Mid	Bottom
27	July	6.8	7.6	7.4	8.8	11.9	10.4
28		6.5	6.6	6.8	8.8	11.5	9.1
29		6.5	6.6	6.0	8.8	11.7	8.6
30		6.1	6.6	6.3	8.8	11.5	8.7
31		6.5	6.6	7.6	10.1	12.2	10.4
3	Aug.	4.5	6.2	4.1	7.0	11.2	6.6
4		5.8	6.3	5.1	8.6	10.5	7.1
5		6.6	7.2	6.4	9.5	12.0	8.7
6		8.0	8.7	8.2	11.2	14.0	11.6
7		7.9	8.1	6.4	10.7	12.8	10.8
8		5.8	6.5	-	8.4	10.2	-

Active Layer Depth

Active layer depth is dependent upon a number of variables which affect the energy reception at the surface and conduction of this energy through the soil body. Energy budget studies of disturbed and undisturbed areas 5 km to the north of this study area (Haag and Bliss, 1973) have shown that albedo, depth of the surface peat layer, and moisture and ice content of the surface horizons are some of the more important factors changed by disturbance. In this study, a comparison of active layers in disturbed and adjacent undisturbed areas showed that active layers were greater in order of the largest difference in: 1) disturbed vs. undisturbed sites, 2) hummocks vs. hollows and 3) mid vs. top or bottom slope positions (Table 7). By the end of the growing season the average active layer depth in disturbed sites is 148% greater than

Table 7. Mean (\pm S.E.) active layer depths in disturbed and adjacent undisturbed hummock and hollow areas at three slope positions during the 1972 growing season.

	S L O P E P O S I T I O N									
	T O P			M I D			B O T T O M			
	Disturbed	Undisturbed Hummock	Hollow	Disturbed	Undisturbed Hummock	Hollow	Disturbed	Undisturbed Hummock	Hollow	
7 June	9.4 \pm 1	8.1 \pm 2	1.6 \pm 0.5	Snow covered	snow covered	snow covered	1.0 \pm 0.4	8.5 \pm 1		2.3 \pm 0.3
13 June	17.7 \pm 1	17.8 \pm 1	3.3 \pm 0.2	17.3 \pm 2	22.6 \pm 1	5.6 \pm 0.5	13.1 \pm 1	15.8 \pm 2		4.6 \pm 0.5
21 June	25.8 \pm 2	25.5 \pm 1	4.4 \pm 1	32.0 \pm 3	31.4 \pm 1	6.8 \pm 0.5	26.1 \pm 1	25.3 \pm 3		6.7 \pm 0.4
4 July	39.4 \pm 3	37.5 \pm 2	8.1 \pm 1	46.2 \pm 4	40.2 \pm 1	11.1 \pm 1	36.5 \pm 1	35.7 \pm 3		9.6 \pm 1
11 July	47.1 \pm 2	40.7 \pm 2	11.4 \pm 1	60.2 \pm 3	45.3 \pm 2	17.6 \pm 2	46.6 \pm 2	40.0 \pm 2		11.4 \pm 1
17 July	51.6 \pm 2	41.7 \pm 2	14.9 \pm 2	65.0 \pm 3	47.6 \pm 1	21.7 \pm 3	45.0 \pm 2	40.2 \pm 2		15.0 \pm 1
24 July	54.5 \pm 2	43.3 \pm 2	20.7 \pm 2	71.6 \pm 3	51 \pm 1	22 \pm 3	50.1 \pm 3	42.5 \pm 2	18	\pm 1.5
31 July	57.0 \pm 1	43.8 \pm 2	23.0 \pm 2	75.2 \pm 3	51.6 \pm 1	26.1 \pm 3	52.2 \pm 3	43.0 \pm 2		22.5 \pm 1
8 August	58.7 \pm 1	44.4 \pm 2	25.2 \pm 2	80.1 \pm 3	51.8 \pm 1	27.3 \pm 3	54.4 \pm 3	43.8 \pm 2		24.0 \pm 2
16 August	60.8 \pm 1	46.2 \pm 1	27.2 \pm 2	83.3 \pm 3	53.3 \pm 1	28.2 \pm 3	54.4 \pm 3	45.1 \pm 2		25.0 \pm 2
21 August	61.6 \pm 1	46.6 \pm 1	27.6 \pm 2	84.2 \pm 3	54.4 \pm 1	29.7 \pm 3	57.2 \pm 3	46.1 \pm 2		26.0 \pm 2

in hollows and 38% greater than in hummocks. The mid-slope position (N2 D2), due to increased isolation and better drainage, has the deepest active layer throughout the growing season. This is most significant in disturbed areas which by the end of the season average 37% greater than the hill-top position and 47% greater than the hill-bottom.

Using N1 D1 as a representative site (Fig. 3) it can be seen that between 7 June and 4 July disturbed areas and undisturbed hummocks achieve the greatest rates of thaw and have nearly equal active layer depths. From 4 July to the end of the growing season both rates decrease, with that of the hummocks showing the greatest decrease, adding only 8 cm of depth compared to 22 cm in the disturbed area. Hollows maintain a relatively low and uniform rate of active layer increase throughout the growing season, achieving the greatest rate during mid-July. This is possibly in response to the attainment of a critical moisture content by the mosses and organic matter within the hollows, decreasing their insulative capacity. In hummocks and disturbed areas 40 to 50% of the maximum thaw occurs in the first two weeks of the growing season compared to only 14% in hollows.

In the clipping experiment (Table 8) the removal of all vegetation from otherwise undisturbed hummocks produced no significant increase in active layer depth, suggesting that the intact peat layer has a greater influence on depth of thaw than either the albedo or insulative effects of living vegetation.

Figure 3. Mean active layer depths (cm) on the hill-top position in both disturbed and undisturbed sites during the 1973 growing season, Tuktoyaktuk Peninsula, N.W.T. Values are means of ten observations (SE \pm 2 cm)

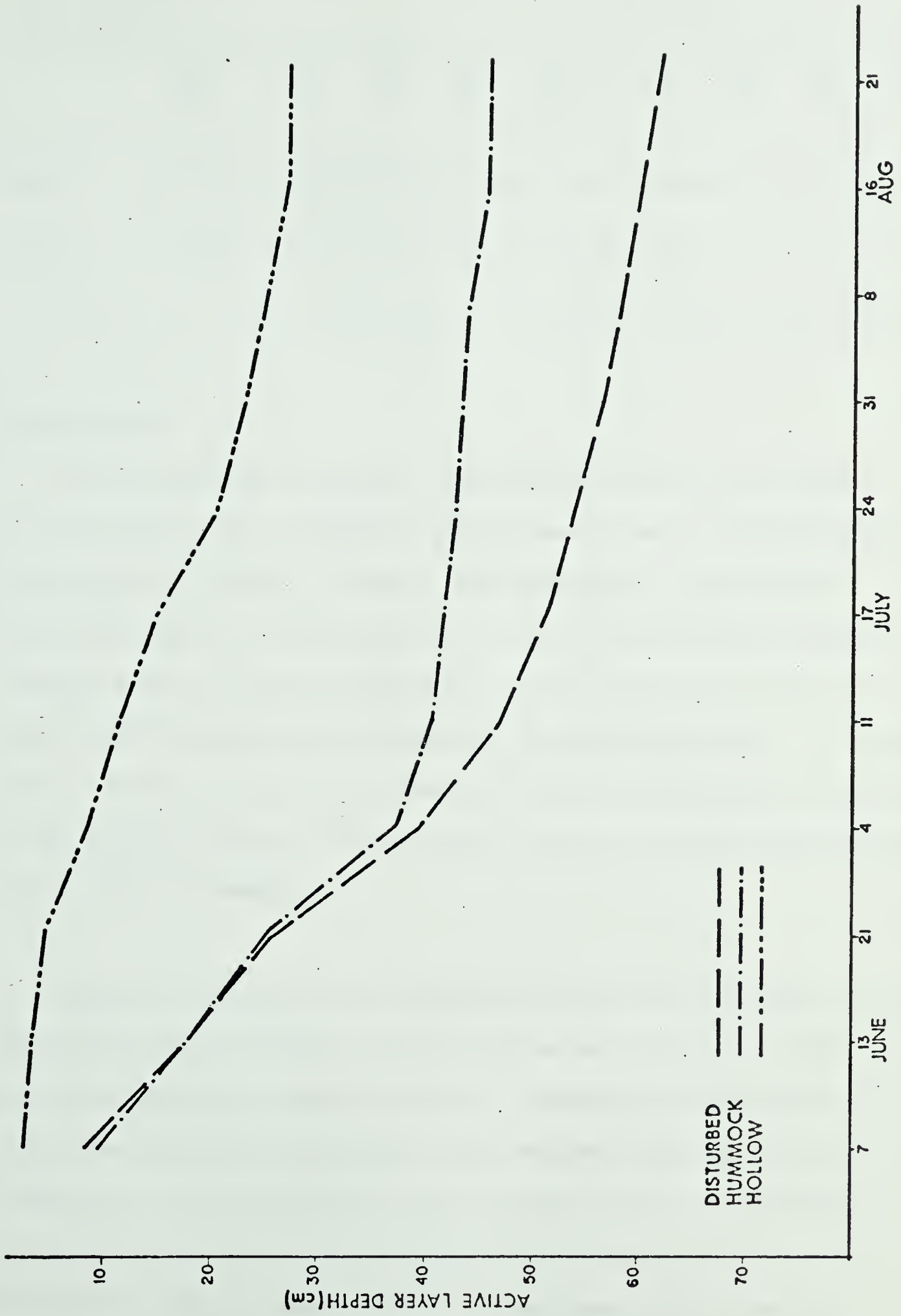


Table 8. Mean (\pm S.E.) active layer depths (cm) of disturbed and adjacent undisturbed (control) hummocks (1972).

	June 15	June 21	July 4	July 11	July 17	July 24	July 31	Aug. 8	Aug. 16
Control	22.2 \pm 2	26.9 \pm 2	36.8 \pm 2	41.8 \pm 2	44.3 \pm 2	45.8 \pm 2	46.6 \pm 2	47.6 \pm 2	49.3 \pm 2
Clipped	19.6 \pm 1	26.6 \pm 1	37.7 \pm 1	39.6 \pm 1	41.9 \pm 1	43.7 \pm 1	44.8 \pm 1	46.4 \pm 1	48.0 \pm 1

Soil Moisture

In the Tuktoyaktuk Peninsula, total precipitation is less than 12 cm per year which in temperate regions would lead to the classification of this area as a desert. However, low temperature, high humidity and the existence of an impermeable frozen soil which impedes internal drainage serves to conserve moisture to such an extent that soils are moist most of the year and soil moisture is seldom considered a limiting factor. Because of the rolling nature of the Tuktoyaktuk area, however, it was believed that soil moisture might change appreciably with topographic position and disturbance.

Seldom did mean soil water potential at any site fall below -3 bars. Expressed as the percentage of total samples below -15 bars, certain general trends became evident (Table 9). Disturbed soils tended to dry to the permanent wilting point more frequently than undisturbed soils (6% vs. 2%) with those at both disturbed (25%) and undisturbed (3% hummock and 10% hollow) mid-slope positions being the driest. Below 10 cm, soils in undisturbed sites were never found below -15 bars, while those in disturbed sites reached this point in less than

3% of the samples. Although the growing season during 1972 was exceptionally dry, receiving less than 50% of normal precipitation, no seasonal drying trend could be observed from the data. The majority of the cases where soils did dry to below -15 bars occurred in late July or August.

Table 9. Percentage of soil moisture samples taken at various slope positions in both disturbed and undisturbed areas which were below -15 bars during the 1972 growing season.

Depth	Hill-top	*Disturbed Mid-slope	Hill-bottom	Total Disturbed
0 - 5 cm	3%	25%	0%	6%
10 - 15 cm	3%	3%	0%	-
		**Undisturbed Hummocks		Total Undisturbed
0 - 5 cm	0%	3%	0%	2%
10 - 15 cm	0%	0%	0%	-
		**Undisturbed Hollows		
0 - 5 cm	0%	10%	0%	-
* 36 samples per site				
** 20 samples per site				

These data suggest that, though moisture is generally plentiful, slope positions have an influence on soil moisture which may be biologically significant. This significance is greatest in disturbed surface soils in the mid-slope position which have the most frequent occurrence of stress below -15 bars. Because the subsurface soils generally have adequate moisture, rooted plants are least affected by surface drought conditions. However, the moisture stress occurring in the surface

layer (0 to 5 cm) may be detrimental to seedlings and germinating seeds.

Snow Cover

The data suggest that disturbance and slope position have a significant influence on snow depth (Table 10). All disturbed areas had greater snow accumulation than adjacent undisturbed areas. The greatest differences were experienced at the mid-slope disturbed site where mean snow depth was 33 cm compared to the snow-free condition of the adjacent tundra. Mid-winter differences were even greater with the disturbed sites averaging 60 to 70 cm more snow than adjacent undisturbed sites (Art Martel, personal communication). This is approximately the same amount that these lines are below the surface of the tundra which shows that blowing snow drifts into these depressions until they come level with the surrounding snow cover.

Biologically this increase in snow cover could be of importance in several ways. During the winter it may serve as a protective insulation to seedlings and less cold hardy plants. In the spring, though it may shorten the growing season somewhat, increased meltwater may aid germination and establishment of seedlings.

Table 10. Mean snow depths (cm) in early June at four slope positions on both disturbed and undisturbed sites.

Treatment	Hill-top	Mid-slope	Lower slope	Hill-bottom
Tundra	snow-free	snow-free	74	snow-free
Disturbed Area	11	33	77	23

Soil Nutrients

Soil nutrient analyses show that the mineral soils within disturbed areas are low in both nitrogen and phosphorus, the available phosphorus content being 0.5 ppm and total nitrogen 0.30 to 0.54%. There appears to be an appreciable amount of available potassium ranging from 80 to 225 ppm. Analyses of the undisturbed surface organic layer (Janz, 1974) have shown similar potassium contents but greater amounts of phosphorus and total nitrogen ranging from 1.9 to 4.6 ppm and 1.1 to 1.5% respectively.

Summary And Discussion

From these data it is clear that disturbance does result in significant changes in the microenvironment, and that these changes are related to both the removal of the insulative turf and the leveling of a hummocky topography. The effect of the latter is most apparent when one considers that hummock soils are only 1 to 3°C cooler than disturbed soils yet 4 to 6°C warmer than adjacent hollows. The warmer hummocks are a result of their hemispherical shape which improves drainage and maximizes the reception of radiant energy. The poorly drained, partially shaded condition of hollows not only leads to a direct reduction of soil temperature but also produces a microhabitat favorable to the growth of bryophytes which further insulate these areas.

Both the removal of turf and the leveling of micro-topography raises temperatures a maximum of 3 to 10°C. The resultant warming leads to an increased active layer and variable slumping or settling as the permafrost ice melts out. The depression formed is filled by

snow in the winter which remains one to two weeks longer in the spring. Soil moisture is not changed appreciably except in disturbed surface soils which tend to reach the permanent wilting point more frequently. The nutrient status of the mineral soil is probably not changed but the nutrient rich reservoir of organic matter is removed. All of these factors, except nutrients, are modified by slope position with disturbed mid-slopes being warmer, drier, and possessing a deeper active layer than ridges or basins.

The biological consequences of these changes will be discussed more fully in the following chapters but certain broad generalization and speculations will be made here. Based upon what is known about temperate plants, many of the changes brought about by disturbance are beneficial. Over winter the increased snow cover in disturbed areas provides an added insulation to seedlings and less cold hardy species. In early spring the added flush of meltwater is beneficial to those species able to germinate and establish under cooler conditions. Drying which occurs as the season progresses allows surface soil temperatures to increase, further stimulating germination and establishment but by mid-July, especially at mid-slope positions, the surface soils are too dry for the germination of most species. However, subsurface soils seldom dry to critical levels so that established species are not stressed. The increase in soil temperature and the concurrent increase in active layer depth favour root and shoot growth. Studies of range grasses grown in cold soils have demonstrated that increases of soil temperature from 7 to 13°C can lead to an increase in biomass of from 400 to 800% (Smoliak and Johnston, 1968).

Possibly one of the more complex changes wrought by disturbance is the effect on soil nutrients. The data of Janz (1974) from the undisturbed organic layer are little different from these gathered from disturbed mineral soils. Both have relatively low amounts of the macro-nutrients, however, the organic horizons are somewhat higher in available phosphorus and total nitrogen. Because of the continued slow release of nutrients by decay organisms it is difficult to evaluate and compare the nutrient status of various areas using samples taken at only one period of time. One of the main effects of disturbance is the removal of the organic mat. Janz and others have suggested that on a weight basis it is here that some of the nutrients are concentrated and from which they are slowly released. It is also here that most of the root systems are located which probably results in a fairly efficient recycling of nutrients with few being leached to the mineral horizon.

Once the organic layer is removed it would appear that most of the nitrogen in the remaining mineral soil is restricted to buried organic inclusions with small amounts being deposited by rain, while the phosphorus content, having its source in the parent material, is dependent upon the type and rate of weathering of parent material. However, disturbance not only removes the organic mat but also allows the soils to warm and the active layer to deepen. This leads to a larger and more favorable medium for root growth and exploitation which may provide a relatively large nutrient supply to those plants able to colonize these areas.

Chapter V

PLANT RESPONSES TO DISTURBANCE

Previous chapters have dealt with descriptions of the preferred habitats of *Arctagrostis latifolia* and *Calamagrostis canadensis* and a characterization of microenvironmental changes brought about by disturbance. The objectives of the studies described in this chapter are to define the response of these species to disturbance in terms of growth habit and morphology, phenology and vigor, net production, leaf water potential, and tissue nutrient content.

Growth Habit and Morphology

General taxonomic descriptions of size, morphology, and ecology of these two species are found in Hulten (1968), Porsild (1964), Tolmachev (1964), Sorensen (1941) and Komarov (1934). Little, however, is known about the response of these species to either natural or disturbed habitats. This section is based upon field observations and measurements made during three summers of field work on the Tuktoyaktuk Peninsula of the growth habit and morphology of these two species in relation to disturbance.

Arctagrostis

In the undisturbed low shrub-heath tundra *Arctagrostis latifolia* is generally restricted to the more deeply thawed tops and sides of hummocks. A single plant normally puts out two to six widely spaced shoots per hummock compared to 75 to 100 shoots in an area of similar size in a disturbed area. The shoots arise from stout rhizomes (5 to 6 mm in diameter), 8 to 10 cm beneath the soil surface. As many

as 8 shoots may branch from a 10 cm section of rhizome in disturbed areas while only one or two from an equal length in undisturbed areas. The shoots are distinctive, being stout (4 to 7 mm diameter) and dark green. They remain tightly rolled until near the third week in June when the first leaf expands. Three more leaves are formed before flower formation. In disturbed areas 70 to 80% of the shoots will produce flowers vs. only 20 to 30% in undisturbed areas. In most cases the shoots die back at the end of the season and are replaced by new shoots the following year.

The root system is comprised of relatively few, stout (1 mm diameter), white to cream colored roots which turn yellow-brown with age. These roots appear to be long-lived, at least surviving two and possibly more seasons. Thus in the early spring, while new roots may be developing in the shallow active layer, the older roots remain encased in the frozen active layer absorbing moisture and nutrients along the retreating active layer permafrost interface. Observations of roots of this species actively growing within several cm of the retreating permafrost table (Bliss, 1956), or even into it (Dadykin, 1958) suggest that metabolic activities are not greatly reduced by low temperatures.

Calamagrostis

Calamagrostis, not being restricted to hummocks or deeply thawed areas, is much more widely spread in the undisturbed tundra than *Arctagrostis*. Shoots are produced by relatively thin (1 mm diameter) rhizomes lying 2 to 5 cm beneath the organic mat. The rhizomes of this species are rather widely spreading and may extend 35 to 50 cm before producing an above-ground shoot. In disturbed areas, shoots are more numerous

but even so a shoot produced at the rhizome may grow 15 to 20 cm horizontally before turning upward. In undisturbed tundra the above-ground shoot is often an indistinctive cluster of 3 or 4 weak, pale green leaves hidden within the dead leaves of previous years' growth. Fewer than 10% of these clumps produce flowering heads. In the disturbed tundra, *Calamagrostis* is much more vigorous producing 40 to 50 shoots per clone with relatively broad, upright leaves. Thirty to fifty percent of the shoots produce flowers. Unlike *Arctagrostis*, many of the *Calamagrostis* shoots only die back to the ground level each year, greening up and continuing to grow the following season.

The root system of *Calamagrostis* is much finer than that of *Arctagrostis*, being more hair-like and having numerous branches. From excavations made in the spring it appears that much of the root system is annual, requiring the regrowth of 70 to 80% each year. A number of short white roots were observed projecting from the rhizomes at the beginning of the growing season. These were much thicker than the normal root and were covered by numerous fine hairs. When pulled gently, an outer covering came off revealing a thread-like inner root typical of the mature root system. Though based on only limited observations, it appears that the thicker outer layer may provide an increased surface area for water uptake prior to the full development of the root system, eventually being sloughed off as the inner root continues to grow.

Phenology and Growth

No detailed phenological studies have been made on either of these grasses, although several authors have reported periods of fruiting and flowering at various latitudes. Klebesadel (1969) observed

Arctagrostis in flower in the Matanuska Valley in south-central Alaska (61°34'N) between early and mid-July with mature seed set between 15 and 25 September. Dennis (1969) working in the Barrow, Alaska area (71°20'N) reported flowering as early as 5 July and immature seed production by 16 August while Sorensen (1941) in NW Greenland (75°N) reported *Arctagrostis* in flower from 16 to 31 July. In the latter two cases little or no viable seed was produced. Sorensen suggested that this was because reduction division in the anthers takes place long after the panicle is exposed, increasing the chances of producing defective pollen. He observed, as had Hodgson (1966) for many Alaskan grasses, that flower bud initiation takes place in the fall and not in the spring as in most temperate region grasses. Thus floral primordia overwinter at least one and possibly two winters before flowering, with flower production during any given season being a function of the environment of the past season.

Little phenological information is available on *Calamagrostis canadensis* and none to my knowledge from arctic regions. Klebesadel (1965) studying fertilizer and harvest responses of native *Calamagrostis canadensis* subs. *Langsdorfii* stands in the Matanuska Valley of Alaska reported that growth was initiated during mid-May. Flower heads were produced in early to mid-July and by the first week in August were in anthesis to early seed production.

Methods

Phenological studies were undertaken during the 1971 and 1972 summer field seasons to determine the timing of growth and development of *Arctagrostis* and *Calamagrostis* as they relate to disturbance and

slope position. In each study site, ten clumps of each species were selected and marked. In each clump the individual shoot to be studied was marked with a toothpick. Observations of growth and phenology of these two species during the 1971 growing season led to the identification of important phenological stages and to the development of a detailed phenological scale similar to that proposed by West and Wein (1971). During the summer of 1972 weekly phenological and height readings were made. Height measurements were made to the extended tip of the uppermost leaf or to the top of the inflorescence whichever was greater. For both grasses the most easily distinguishable phenological characters were the number of expanded leaves, flower in the boot, floral emergence from the boot, anthesis, seed ripening and seed dispersal. A whole number was used to represent each stage. Leaves which were expanded but not yet reflexed were expressed as halves (i.e. 2.5 or 3.5) and the degree of emergence from the boot and anthesis was expressed in tenths.

In 1972 a study was also initiated to determine the effect of competition on phenology and growth. This study was done in conjunction with the active layer depth study described earlier. At the hill-top undisturbed position ten hummocks containing clones of *Arctagrostis* were selected and completely cleared of all vegetation and roots down to about 2 cm within a 45 cm radius of each clone. The peat layer was left in place and the *Arctagrostis* clones were left undisturbed. Growth and phenology were studied as previously described. The results were compared with those from the undisturbed *Arctagrostis* clones previously marked at that position.

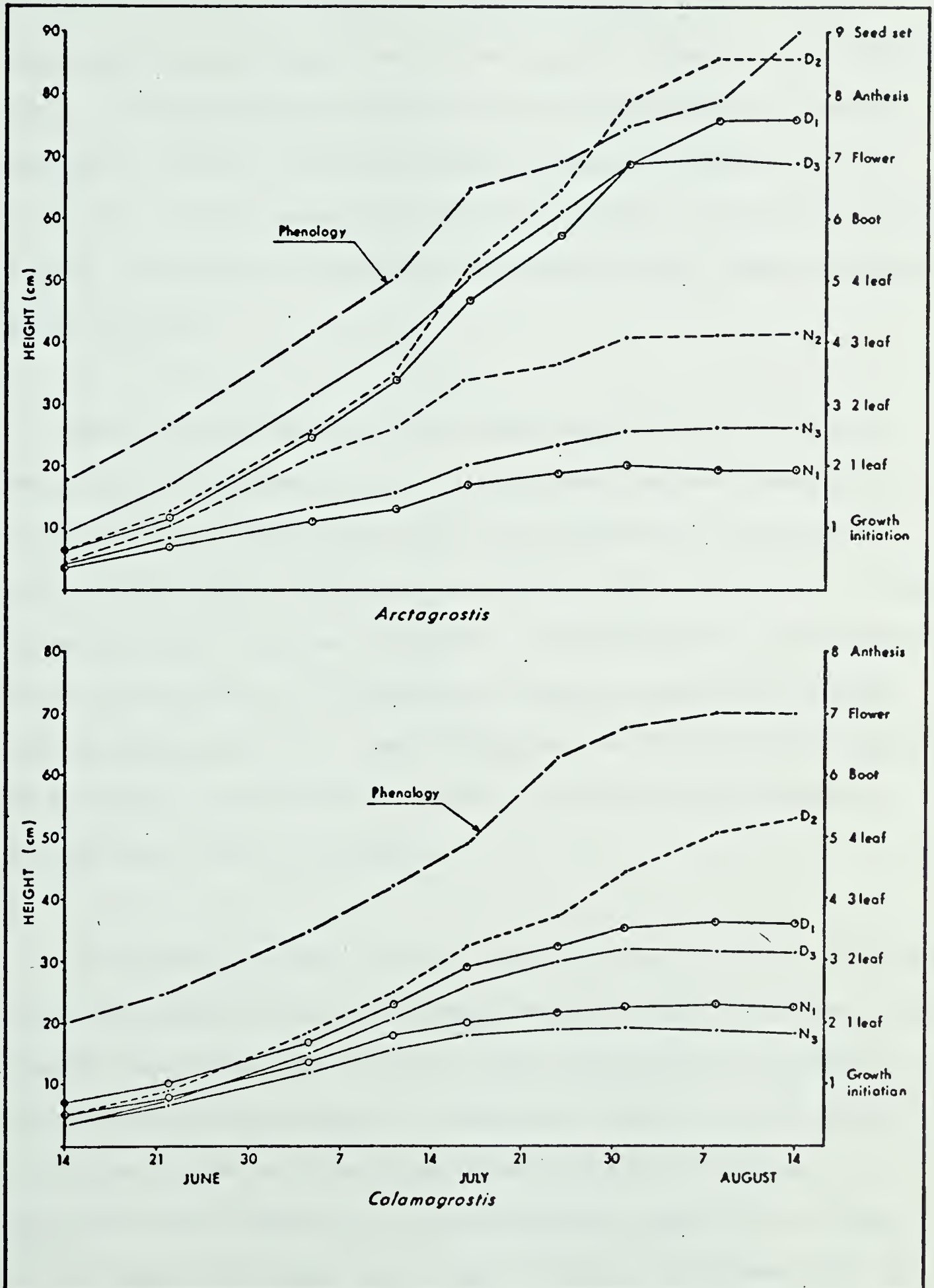
Results

Growth

The greatest and most rapid growth for both species was made in disturbed areas (Fig. 4). During the 1972 field season *Arctagrostis* attained heights of 70 to 80 cm in disturbed areas vs. 20 to 40 cm in adjacent undisturbed areas while *Calamagrostis* reached heights of 30 to 50 cm in disturbed areas vs. 17 to 25 cm in undisturbed sites. The greatest rate of increase generally occurred during the first two weeks in July. After this period, for species in the undisturbed tundra, there was a gradual reduction in growth rates with a leveling off for *Calamagrostis* by mid-July and for *Arctagrostis* by the end of July. In disturbed areas, partially due to the increased number of plants which produced flowering culms, growth continued for both species until 8 August.

The mid-slope position in both disturbed and undisturbed sites produced the tallest plants. *Arctagrostis* was an average 12 and 17 cm taller in disturbed and undisturbed mid-slope positions respectively. *Calamagrostis* was an average 16 cm taller in the disturbed mid-slope position, however, too few plants were found at the undisturbed mid-slope position to make valid comparisons. The increased growth in disturbed areas and especially in mid-slope areas appears to be related to both the increased active layer depth and soil temperature found in these areas. A high correlation ($r = .92$) was found between plant height and active layer depth. *Arctagrostis* showed the greatest response to disturbance, having an average increase over individuals in undisturbed areas of 165% while *Calamagrostis* had an average increase of 65%.

Figure 4. Mean plant heights at hill-top (1) mid-slope (2) and bottom-slope (3) positions in both disturbed (D) and undisturbed (N) areas and mean phenological stage averaged over all areas, of *Arctagrostis* and *Calamagrostis* plants on the Tuktoyaktuk Peninsula during the 1972 growing season.



Phenology

Phenology was originally expressed as the mean phenological state of the ten individuals marked at each site in 1972. This resulted in disturbed areas being shown as phenologically advanced over undisturbed areas. It became apparent however that this advancement was due to the greater number of individuals that flowered in disturbed areas, a function of vigor rather than advanced phenology. To alleviate this problem, phenology as expressed here is based on only those individuals which flowered.

Seasonal phenological data for both species averaged over all positions are displayed in Fig 4. Statistical analysis revealed that for *Arctagrostis* there is no significant difference in phenological stage between plants growing in disturbed or undisturbed sites or among slope positions. Too few *Calamagrostis* plants flowered at any location to run reliable tests of significance, however a comparison of those that did flower shows only small differences in flowering stage suggesting that, similar to *Arctagrostis*, there is little effect on phenology of slope position or disturbance.

Initiation of growth occurred in the first week of June. Phenologically, both species advanced uniformly until the 11th of July when *Arctagrostis* reached the four leaf stage while *Calamagrostis* was still in the three leaf stage (Fig. 4). *Arctagrostis* advanced rapidly during the following week with most plants having flowers in the boot and some plants even flowering. Most *Arctagrostis* plants were in flower by the third week of July while those of *Calamagrostis* were still in the boot. During the next two weeks, plants of *Arctagrostis* were in

various stages of anthesis, the florets at the base of the inflorescence maturing first. Seed development was completed by the middle of August with seed ripening completed by the end of August.

Calamagrostis heads were fully extended from the boot by the end of July but the inflorescence remained tightly closed for two more weeks. Many inflorescences were spreading and open by the middle of August with anthesis just beginning. Anthesis lasted at least two weeks with fruit ripening beginning near the first week in September. Seed collection was made on the 14th of September. At this time *Arctagrostis* was fully ripe and seed dispersal had begun. *Calamagrostis* seed was still in the milk stage and dispersal had not begun.

Disturbance had a significant effect on plant vigor as expressed in flower abundance and seed production. In disturbed sites 86% of the randomly selected *Arctagrostis* plants flowered vs. only 29% in undisturbed sites. Far fewer plants flowered for *Calamagrostis* with only 35% bearing flowers in disturbed areas vs. 10% in undisturbed areas. For both *Arctagrostis* and *Calamagrostis* the most prolific flowering occurred in the disturbed mid-slope position. Seed production for *Arctagrostis* was considerably greater in disturbed areas with an average of 32 ± 33 seeds per head vs. 67 ± 10 in undisturbed areas. Greatest seed production took place at the disturbed mid-slope position which had an average of 680 ± 99 seeds per head. In both disturbed and undisturbed areas seed production for *Calamagrostis* was highly variable with a mean of 50 and a range of from 0 to 150 seeds per head. This may be related to the extended period of anthesis near the end of the season which may result in damage to the germ cells.

In the competition study, a comparison of final heights and phenological stages of *Arctagrostis* plants revealed no significant differences due to the removal of surrounding vegetation. The mean phenological stage on both cleared and uncleared hummocks was the three leaf stage with plants on cleared hummocks having a mean height of 13.1 ± 1 cm vs. 13.7 ± 1 cm on uncleared hummocks.

Net Annual Production

Measurements of above-ground standing crop and annual production in arctic and alpine tundras have been made by Thompson (1955), Bliss (1956, 1962a, 1962b, 1966), Warren Wilson (1957), Billings and Bliss (1959), Dennis (1969) and many others. These measurements have shown for the most part that though daily increments may equal or even exceed those of temperate regions, seasonal totals are generally far short of those for most temperate communities (Billings and Mooney, 1968). Though annual above-ground vascular plant production is quite variable in the various tundra ecosystems, ranging from a low of 3 g/m^2 for *Salix arctica* barrens on Cornwallis Island to a high of 190 to 224 g/m^2 for *Dupontia fisheri* wet sites at Point Barrow, Alaska, most figures lie between 40 to 128 g/m^2 (Bliss, *et al.*, 1973).

Authors disagree as to the basic reason for the low productivity. Wager (1941) identified low temperature with resultant low carbohydrate production. Dennis (1969), studying root and shoot production at Barrow, Alaska, found root: shoot ratios of from 5:1 to 14:1, considerably higher than those for comparable temperate region plants. He suggested that the decrease in size of the ratio from arctic to temperate regions was the result of an arctic environment which is relatively more severe

for above-ground than for below-ground production. Sorensen (1941), Russell (1940), Warren Wilson (1954) and Haag (1974) have presented evidence which suggests that soil nutrients and especially low levels of nitrogen have been responsible for low productivity. In a more recent paper Warren Wilson (1966) suggested that, though levels of soil nitrogen emphasize the problem, low production is primarily a result of low air temperatures which slow the rate of incorporation of photosynthates into new plant tissue, leading to a build up of assimilates and a depression of further assimilate production, but my growth chamber studies and field studies of Allesio and Tieszen (1973) do not confirm this.

Methods

During the 1972 growing season net production was measured in the 1965 seismic line for *Calamagrostis* and *Arctagrostis* to provide information on the effect that disturbance has on above-ground production. The area selected for measurement was on a 5% northwest-facing slope. The slope was divided into top, mid, and bottom and systematically sampled using a 2x5 dm quadrat to determine percent cover of the two species. Above-ground production was sampled using a 0.5 dm circular ring. At each sampling period seven samples were taken in each of the three slope positions in areas which contained 100% cover of either species. This was easily done since both species form relatively dense, pure clumps. The samples were clipped to ground level, placed in paper bags and dried for 24 hr at 80°C. Living and dead tissue was separated and placed in paper bags. All samples were redried for 24 hr and weighed in the laboratory.

Results

The data show that disturbed areas on the Tuktoyaktuk Peninsula invaded by *Arctagrostis* and *Calamagrostis* are highly productive (Table 11). Based upon only two species which together made up 15% of the 25 to 35% total plant cover (the remaining plant cover was primarily mosses - 10 to 15% and vascular plants such as *Poa lanata*, *Carex Bigelowii* and *Stellaria monantha* - each 2%), net annual above-ground production was 280 g/m^2 , 227 g of which were produced by *Arctagrostis*. This is close to the 300 to 400 g/m^2 reported for temperate prairies (Coupland, 1972) and far higher than that reported for any undisturbed tundra ecosystem. Studies by Haag (1974) of an undisturbed low shrub-heath community on the Tuktoyaktuk Peninsula, similar to the one disturbed on the 1965 seismic line, showed a production of $60 \text{ g/m}^2/\text{year}$ or only about 20% that of the disturbed area. If only grass or grass-like species are considered (*Arctagrostis*, *Calamagrostis*, *Carex*, and *Hierochloe*) the annual production is only 4 g/m^2 or 1.5% of that in the disturbed area.

Table 11 Mean \pm SE net production and percent ground cover of *Arctagrostis* and *Calamagrostis* in a 1965 seismic line on the Tuktoyaktuk Peninsula during the 1972 growing season.

Species	% cover	Net Production (g/m^2)		
		20 June	20 July	20 August
<i>Arctagrostis latifolia</i>	8	2 ± 0.2	$118 \pm 7.$	$227 \pm 16.$
<i>Calamagrostis canadensis</i>	7	-	-	$53 \pm 4.$

Plant Water Potentials

Few investigations have been made of the water relations of arctic species, partially because of a lack of accurate field techniques and a belief that in the vast expanse of poorly drained tundra, plants are seldom under a water stress. Recent improvements in equipment and technique and a greater interest in arctic regions have resulted in the examination of water potentials for a number of species. Many of these studies, both in alpine and arctic tundras, are reviewed by Courtin and Mayo (1974). Though the results are not always in agreement, it appears that for many species, water potentials are much more negative than previously expected, raising the question of what constitutes a water stress for arctic plants.

Dennis (1969) working in Alaska and using the Shardakov dye method has reported the most positive leaf water potentials (ψ) of the recent investigations. Of the twenty species tested, few showed water deficits of less than -2 bars. *Arctagrostis latifolia*, examined in a number of habitats, never showed a water deficit of less than -4 bars. Haag (1972) using a Wescor Microvoltmeter and Sample Chamber Psychrometer found water potentials on the Tuktoyaktuk Peninsula of -20 to -25 bars for *Betula nana* and *Vaccinium vitis-idaea* plants growing in relatively well-drained upland sites and -25 to -35 bars for *Carex rariflora* and *Eriophorum russeolum* plants growing in standing water. Teeri (1973) studying *Saxifraga oppositifolia* growing on raised beach ridges on Devon Island reported tissue water deficits ranging from -6 to -44 bars. Laboratory studies revealed that net photosynthesis remained positive at potentials of -21 to -29 bars and that the plant could survive tissue water stresses of as great as -55 bars. *Dryas integrifolia*,

another plant found on raised beach ridges on Devon Island, had leaf water potentials of from -30 to -37 bars even when soil water potentials were only or less than -5 bars (Courtin and Addison, 1972). In the boreal forest region, Small (1972) employing the pressure bomb psychrometer on evergreen bog plants found that many plants growing in standing water had water potentials of from -10 to -20 bars.

Methods

In the present study, plant water potentials were examined to determine the effect disturbance had on tissue water stress. It was hypothesised that a reduction in total plant cover and therefore competition as a result of disturbance would lead to a lowering of the water stress of the remaining individuals.

Leaf water potentials were measured using a Wescor Microvoltmeter and Sample Chamber Psychrometer. Only tissues from *Arctagrostis latifolia* growing in the disturbed and undisturbed hill-top position were tested. The days during sampling (12, 13 and 19 July) were clear and warm with the 12th and 13th being very windy and the 19th relatively calm. Because previous testing had shown that tissue water potentials varied not only between leaves on the same plant but also between sections from the same leaf, the tissue selection procedure was standardized. Plants selected were all in the same approximate phenological stage i.e. 2 or 3 leaf stage. Only tissue from the very base of the upper-most leaf blade was used. Leaf tissue temperature was measured using a fine wire thermocouple and then the leaf was cut and placed in the sample chamber. To reduce temperature fluctuations, the sample chamber was placed in a styrofoam box during the equilibrium time of 20 min.

After each run the sample holders were cleaned, and allowed to dry. The sampling period was between 9 AM and 4PM. Tissue water potentials for plants from disturbed and adjacent undisturbed tundra taken during the same time interval were compared using a paired "t"-test.

Results

Water potential readings ranged from -10 to -19 bars, similar to those of other studies (Haag, 1972; Teeri, 1973; Courtin and Addison, 1972; Small, 1972) but lower than expected as soil moisture measurements had shown that soils in both areas were close to field capacity throughout the growing season. The water potentials of plants growing in undisturbed tundra were consistently more negative than those of plants growing in disturbed areas. Mean ψ plant in undisturbed areas was -15 bars vs. -11.1 bars in disturbed areas, the difference being statistically significant at the 99% level. The biological significance of this is uncertain however as in neither case were there obvious signs of water stress such as wilting or leaf rolling.

Tissue Nutrient Contents

Tissue nutrient contents suggest something of the conditions under which a plant has grown, indicating not only what nutrients are present in the soil but also to some extent the amounts present or the degree to which they are available. In the latter, the relationship is complex and is open to some interpretation. Studies have suggested that nutrient levels probably remain stable within a plant as long as no other factors are limiting and nutrient additions are allowed to express themselves as dry weight increases (Corns and Schraa, 1962). Increased concentrations

are believed to occur when additions are made beyond that necessary to stimulate increased yields or possibly when production is limited by some other factor (Sullivan and Wilkins, 1948).

In the Arctic, as in other areas, nutrient contents have primarily been of interest in the determination of the forage potential of selected species. Scotter (1972) studying the monthly nutrient changes of nine forage species collected from the Reindeer Reserve near Inuvik, N.W.T. found that protein contents were low in most plants by mid-winter while phosphorus was low throughout the year. *Arctagrostis latifolia* showed a nitrogen and phosphorus content of 1.4% and .15% respectively in July before flowering and .83% and .09% respectively in August after flowering. *Arctagrostis latifolia* var. *arundinacea* grown in fertilized gardens at Palmer, Alaska had a mean nitrogen content of 2.8% in contrast to the 2.4% of the two agronomic species, Engmo timothy and Polar bromegrass, with which it was compared (Klebesadel, 1969). In Arctic USSR, native populations of *Arctagrostis latifolia* were found to have nitrogen contents of 2.2% in August prior to fruit development and 1.2% in September after fruit development (Aleksandrova *et al.*, 1964). In comparison, native populations of *A. arundinacea* (Hulten's *A. latifolia* var. *arundinacea*) were found to have nitrogen and phosphorus contents of 3.1% and .36% respectively in July and 1.6% and .37% respectively in August after fruiting.

No information was found concerning nutrient contents of *Calamagrostis canadensis* from arctic regions. Field collections made in the subarctic near Palmer, Alaska in July showed nitrogen and phosphorus contents of 2.3% and .18% respectively (Laughlin, 1969).

Janz (1973) studying trends in nutrient contents of native vegetation along hill-sides in the Mackenzie Delta region found that standing crop nitrogen contents ranged from .84% to 1.1% and phosphorus contents from .10% to .08%, both decreasing from hill-top to hill-bottom. Available soil nitrogen was not found to change with slope position suggesting that plant nitrogen contents were affected by some other factor than available soil nitrogen.

Methods

Tissue samples in both disturbed and undisturbed areas were collected for *Arctagrostis* at three times during the growing season and for *Calamagrostis* at the end of the growing season. Samples were randomly selected, clipping off the plant at the soil surface. The plants were dried for 24 hr at 80°C and then stored in paper bags at room temperature. Prior to analyses the plants were re-dried and sorted into leaves and culms. The separated parts were ground to pass through a 60 mesh sieve, thoroughly mixed and subsamples selected and sent to the Alberta Soil and Feed Testing laboratory for nutrient analyses of nitrogen, phosphorus and calcium. Nitrogen was determined by the macro Kjeldahl method, phosphorus by the vanado-molbdate method and calcium by the oxalate titrimetric method.

Results

Individuals of both *Arctagrostis latifolia* and *Calamagrostis canadensis* growing in disturbed sites were considerably richer in nitrogen and phosphorus than plants of the same species growing in undisturbed tundra (Table 12). The mean increase was greatest for *Calamagrostis*, ca. 120% for both nitrogen and phosphorous while for *Arctagrostis* the mean

Table 12. Nutrient contents (% dry wt) of Arctagrostis latifolia and Calamagrostis canadensis leaves collected from disturbed and undisturbed sites on the Tuktoyaktuk Peninsula, N.W.T.

Date	Site	N (%)	P (%)	Ca (%)
<u>Arctagrostis latifolia</u>				
20 June	Disturbed	4.09	.64	.16
19 July	Disturbed	2.91	.28	.30
19 July	Hill Top undisturbed	1.96	.17	.27
19 July	Hill Base undisturbed	1.87	.16	.27
18 August	Disturbed	2.92	.21	.42
18 August	Hill Top undisturbed	1.37	.11	.36
18 August	Hill Base undisturbed	1.23	.13	.40
<u>Calamagrostis canadensis</u>				
18 August	Disturbed	2.10	.20	.28
18 August	Hill Top undisturbed	1.11	.12	.37
18 August	Hill Base undisturbed	.79	.06	.37

increase was approximately 80% for nitrogen and 70% for phosphorus. There was no significant or consistent difference in either species for calcium.

Plants growing on the hill-top had small but consistently higher levels of nitrogen and phosphorus than those at the base of the hill. These differences, similar to those reported by Janz (1974), were largest for *Calamagrostis*, the hill-top plants having 40% and 50% greater levels of nitrogen and phosphorus respectively.

The nutrient content of *Arctagrostis* was followed over the season. The highest levels of nitrogen and phosphorus were recorded in late-June, just prior to the period of rapid growth. Calcium content was lowest at this time but increased as the season progressed, probably as a function of increasing fiber content. Nitrogen and phosphorus levels of plants growing in the undisturbed tundra dropped 30% and 35% respectively after the period of flowering and fruit production. This is similar to the observations of Scotter (1972) and Aleksandrova *et al.* (1964). However in the disturbed tundra this large decrease was not observed, nitrogen levels remained unchanged and phosphorous decreased only 25%.

Summary and Discussion

The above data suggest that in almost all cases, disturbance had a positive influence on growth and vigor of both species. Plants growing in disturbed areas had 15 to 50 times more shoots per clone, 3 to 5 times more flowering heads, up to 5 times more seeds per head and mean

increases in plant height ranging from 65% to 165%. For all of these factors the largest absolute increases occurred at the disturbed mid-slope position except for clone size, which was generally the same at all positions, and seeds per head for *Calamagrostis*, which were variable and low at all locations. Perhaps the best integrator of the factors suggesting increased vigor is net annual production which in disturbed sites increased almost five times from 60 g/m^2 to 280 g/m^2 .

Both species had significantly higher concentrations of nitrogen and phosphorus in disturbed sites. Although slope comparisons were not made among disturbed sites, plant tissues gathered in undisturbed sites showed a slight but consistent decrease in both elements from top to bottom of the slope. Water potentials of *Arctagrostis* growing in undisturbed sites was an average 4 bars higher in plants in undisturbed sites. The lack of any growth stimulation when the surrounding vegetation was removed from clones of *Arctagrostis* suggests that plant competition was either not the cause of water stress or that water stress was not the primary cause of the reduced vigor.

Although *Arctagrostis* and *Calamagrostis* are similar in size in southern latitudes (Hulten, 1968), on the Tuktoyaktuk Peninsula, *Arctagrostis* is clearly the larger and more vigorous species, producing 2 to 3 times as many flowering heads, 50 to 150 times as many seeds per head and 80% of the total net production of these two species in disturbed areas. Rate of phenological development is not affected by disturbance or slope position, however, the development of *Arctagrostis* is in advance

of *Calamagrostis*, having seed set by the middle of August while *Calamagrostis*, is just beginning anthesis. This delay in seed set may explain the small and variable seed production observed in *Calamagrostis* as late August and early September are frequently cold and windy on the arctic coast, possibly reducing pollen viability, as well as reducing the time available for seed maturation.

Many authors have discussed the problem of limiting factors in the North in an attempt to identify the reason or reasons for the generally low yearly production. At different times and in varying combinations physiological aridity, soil nutrient deficiencies or heat deficits have been proposed as contributing factors (Schimper, 1898; Sorensen, 1941; Russell, 1940; Dadykin, 1958; Dennis, 1969; Polunin, 1955; Bliss, 1956, 1962; Warren Wilson 1954, 1959, 1966). The present data suggest that some microenvironmental change related to disturbance results in a greatly increased productivity. Although purely speculative at this point, the identification of the factor or factors involved may provide a basis for future laboratory research.

As discussed previously (see Chapter 4) the data suggest that increases in active layer depth and soil temperature are the most significant environmental changes resulting from disturbance. How these changes may affect production is not yet clear though it seems obvious that neither adds nutrients to the soil (the nutrient rich organic layer is removed) or leads to large increases in air temperature.

Though the plants in disturbed areas are under a significantly reduced water stress, the mean difference of 4 bars does not appear large enough to warrant the 5-fold increase in plant production, although until component potentials are examined, the magnitude of this cannot be stated with certainty. Soil nutrient data suggest that disturbance does not significantly change the amounts of nitrogen or phosphorous in the soil, yet tissue nutrient analyses show that plants growing in disturbed areas are significantly richer in both of these nutrients. This indicates that some factor or factors associated with disturbance have increased nutrient availability.

Based on the environmental factors previously mentioned, an increase in nutrient availability could be accomplished in a number of ways. Increases in soil temperature could lead to increase in microbial activity, water availability and absorption, root respiration and root growth, while an increase in the active layer would result in an increase in the volume of soil available for root exploration. No doubt all of these factors play some role in the improved growth and mineral nutrition of these grasses, however, some would appear to be more important than others. Increased microbial activity is probably of relatively minor importance. Except for pockets or layers of buried organic matter the soils in disturbed areas are mineral. Though past research has shown that water viscosity increases and cell plasma permeability decreases with decreases in temperature (3 to 7°C) (Kramer, 1940) the present findings suggest that cold soils do not greatly restrict water uptake in arctic species. Increased root respiration and a concomitant increase in the active uptake of minerals is likely with an increase in soil

temperature, however, recent studies of *Eriophorum vaginatum* (Chapin, 1972) suggest that species adapted to cold soils have no special metabolic system for mineral uptake at low temperatures, but instead rely on an ability to increase the size of the absorptive surface area at low soil temperatures. If the latter is the case, the ability for rapid root growth as soils warm, coupled with a greatly increased volume of unfrozen soil, could result in a very substantial absolute increase in nutrients. The influence of cold soils on a number of these factors including plant growth and development, nutrient accumulation, tissue water potentials and photosynthetic rate were tested in the laboratory and will be discussed in the following chapters.

Chapter VI

SEED GERMINATION

The seed represents one of the most unique stages in the life cycle of a plant, for it is in this stage that life is held in suspension (Amen, 1964) awaiting, in some cases thousands of years (Porsild *et al.*, 1967), those conditions which will initiate plant growth. While in the dormant state, the embryo is protected from much of the stresses of its environment, but once dormancy is broken and germination begins, the developing seedling is committed to growth and is exposed to the rigors of its environment. Success of the young plant hinges on the rapidity, in the face of many environmental variables, with which the germinating seed can develop and establish a self-supporting root and shoot system.

The role of the seed in temperate ecosystems is well documented. In these areas, the climate is such that the seed has remained an important form of dispersal and reproduction, its success being limited more by space in the community than by a lack of heat or moisture. In arctic and alpine ecosystems, seeds face not only the problem of a possible closed community but also a relatively harsh environment characterized by a cool, short and often arid growing season. Environmental severity and the small numbers of seedlings observed in many tundra areas (Bliss, 1958; Amen, 1966) have led many investigators to demphasize the importance of the seed in reproduction in favor of vegetative means.

Early germination studies of tundra species concentrated on the role and importance of seed dormancy mechanisms. Soyrinki (1938) and

Sorensen (1941) demonstrated that in over 66% of the nearly 100 species tested from Lappland and Greenland, no pretreatment was required to stimulate germination. These studies established the now generally accepted principle that dormancy for most tundra species is controlled by external environmental factors and not by internal mechanisms (Bliss, 1958, 1970; Billings and Mooney, 1968). More recent studies by Amen (1966) have suggested that when internal dormancy mechanisms do exist, such as seed coat inhibition, they are most often possessed by the dominant species in the vegetation. Most are easily overcome by scarification or stratification (Billings and Mooney, 1968). Some forms of germination inhibition have been associated with the habitat preference of the species. Bliss (1958) found that most species occurring on deeply thawed soils had seeds which germinated easily, doing so equally well in light or dark while of those species normally found on shallowly thawed soils, less than half produced seeds easily germinated, 75% of which did not germinate in the dark.

While many germination experiments have been carried out at room temperature (Bliss, 1958; Bonde, 1965; Amen, 1965), increasingly tests have been made of germination response to a range of both constant and fluctuating temperatures (Spomer and Salisbury, 1968; Sayers and Ward, 1966). Most of these tests have suggested that optimum temperatures for speed and completeness of germination are between 20 to 30°C (Billings and Mooney, 1968; Sayers and Ward, 1966), comparable to the temperatures at which most temperate and tropical species germinate. While the early germination experiments of De Condole and Seynes showed that many cereal and garden crops such as wheat, rye, cabbage and beans

could germinate at the temperature of melting ice (Coffman, 1923) only one instance has been reported of a tundra species germinating at a constant temperature of 5°C (Billings and Mooney, 1968). While there appears to be some evidence that low fluctuating temperatures are more favorable to germination than low constant temperatures, more research is needed.

The objectives of the present research were: 1) to determine the germination response of *Arctagrostis latifolia* and *Calamagrostis canadensis* under various environmental conditions and 2) to compare this response with both tundra and commercial strains of northern species in an attempt to better understand the reasons for their successful colonization of disturbed areas.

Methods

Germination experiments in the field were conducted under ambient conditions in Petri dishes on moist filter paper. In the laboratory, experiments were conducted to determine the effects of temperature, moisture, and light on germination. Most germination experiments were run within six months of seed collection and, unless otherwise specified, all data are from collections made near Tuktoyaktuk, N.W.T.

Temperature experiments were conducted on a seed germination bar which provided a temperature gradient between 5 and 20°C. Seeds were placed in filter paper lined aluminium containers which were placed on the bar at 5°, 10°, 15° and 20°C. For temperatures above 20°C a Controlled Environments (model #GERM) growth chamber was used, set

at the desired temperature. Temperature within the trays was monitored using fine wire thermocouples and maintained at the desired temperature ($\pm 1^{\circ}\text{C}$). Distilled water was added to keep the seeds moist and continuous light (250 ft-c) was provided by a bank of fluorescent lights.

To simulate conditions of physiological aridity, different concentrations of Manitol solution were used (Uhvits, 1946). Three water potentials were selected; 0 bars, -3 bars and -6 bars. Seeds were cleaned and placed in Petri dishes with equal amounts of the appropriate solutions. Each Petri dish was weighed to the nearest 0.01 g and then weighed every other day and brought back up to the original weight by the addition of distilled water. No Petri dish lost more than 0.5 ml during these periods. All samples were placed in a seed germinator at 20°C with continuous light. After 35 days germinated seeds were counted and ungerminated seeds were rinsed with distilled water and returned to the seed germinator. After an additional 25 days, germinated seeds were counted and added to the initial germination counts for the calculation of total percent germination.

Cold treatment of selected species was provided by a 14 day period between moist filter paper at 2°C . Tests of dark germination were conducted at room temperature (20 to 23°C) in a photographic dark room in blackened Petri dishes. The latter were exposed to 30 minutes of light every five days during examination.

In all germination tests, seeds were checked every other day at which time germinated seeds were removed. A seed was considered germinated when the coleorhiza appeared. Most tests involved three replicates

of 25 seeds each; however, this varied from one to twelve replicates per test. Percent germination is based on the number of seeds which germinated at the end of 35 days for laboratory tests, and after 15 to 20 days for most field experiments. The coefficient of velocity of germination is based on the time required to germinate up to 15 seeds (Dubetz, *et al.*, 1962) and gives an indication of the rate of germination. It is highest for seeds that germinate in the shortest time, and least for seeds requiring the longest time for germination. Significance was determined (F test) using a completely randomized design. Treatment effects were ordered using the Duncan's Multiple Range test (Steel and Torrie, 1960).

Results

Germination of Tundra Species

The data in Table 13 are the result of germination tests conducted over a three year period. The assignment of a species' importance to undisturbed tundra, disturbed tundra or combined categories is based on both field observations and the results of the habitat studies described in Chapter 3.

Seeds of species important in disturbed sites share several common features. They have relatively high germination percentages, require no pretreatment, and germinate under normal temperature and moisture conditions. Species important in the undisturbed tundra or nearly equal importance in both sites have a much lower percent germination, which in all cases, except for *Betula nana* ssp. *exilis* remained unchanged

Table 13. Range of germination percentages for species found on the Tuktoyaktuk Peninsula. The data include germination percentages under field and laboratory (20°C) conditions. The area of species importance in the tundra is shown by: N = native tundra, D = disturbed tundra and ND = native and disturbed tundra.

Species	Tundra Importance	Field	Germination (%)		
			non-stratified	Laboratory cold stratified	
<i>Betula nana</i> ssp. <i>exilis</i>	N	15 to 20	20 to 30	50 to 70	
<i>Eriophorum vaginatum</i>	N	35 to 50	20	20	
<i>Lupinus arcticus</i>	N	--	8 to 25	8 to 25	
<i>Pedicularis lanata</i>	N	0	0	0	
<i>Hierochloa alpina</i>	N	4	--	--	
<i>Saussurea angustifolia</i>	N	0	--	--	
<i>Carex Bigelowii</i>	ND	0 to 5	0 to 5	0 to 5	
<i>Rumex arcticus</i>	ND	35	8 to 32	--	
<i>Luzula confusa</i>	ND	0	0 to 5	--	
<i>Dryas integrifolia</i>	ND	16 to 40	90 to 95	--	
<i>Ranunculus gmelinii</i>	ND	--	8 to 14	--	
<i>Calamagrostis canadensis</i>	D	--	70 to 80	70 to 80	
<i>Arctagrostis latifolia</i>	D	65 to 75	80 to 90	80 to 90	
<i>Poa lanata</i>	D	65 to 95	90 to 100	--	
<i>Festuca brachyphylla</i>	D	60 to 90	80 to 90	80 to 90	
<i>Senecio congestus</i>	D	--	80 to 90	--	
<i>Epilobium angustifolium</i>	D	--	90 to 100	--	
<i>Agropyron latiglume</i>	D	24	60 to 90	--	
<i>Stellaria monantha</i>	D	0	32 to 60	--	

by cold treatment. Seeds of evergreen shrubs such as *Vaccinium vitis-idaea* ssp. *minus* and *Empetrum nigrum* ssp. *hermaphroditum* which are important in the undisturbed tundra were not tested, but studies by Bliss (1958) of these and other species in the Umiat, Alaska area showed no germination.

Response to Temperature

Several species important in the undisturbed tundra, *Eriophorum vaginatum*, *Carex Bigelowii* and *Betula nana* ssp. *exilis*, have both a low percent and slow rate of germination at 20°C (Table 14). Only *Eriophorum* was tested at lower temperatures but showed no germination below 20°C. Wein and MacLean (1973) testing *Eriophorum vaginatum* populations from Inuvik, N.W.T. and near the lower Rat River, Y.T. found 60% and 70% germination respectively at 20°C, but also found no germination below 20°C. They noted that over a storage period of as short as three months, seed viability decreased significantly.

Of the grasses tested, *Poa lanata* and *Arctagrostis latifolia* have the highest and most consistent germination percentages at all temperatures. *Festuca brachyphylla* and the two agronomic species, *Festuca rubra* and *Poa pratensis*, have high percentages of germination above 5°C, but these drop significantly at 5°C.

Germination rates in all species decreased with reduced temperature, the greatest decrease taking place between 10°C and 5°C. Of the grasses, germination rates were least in *Festuca brachyphylla*, which had a very low rate at all temperatures. *Arctagrostis latifolia* had the highest

Table 14. Mean percent and rates (\pm SE) of germination of selected species as affected by temperature. Percent germination is based on the number germinated at the end of 35 days. Rates are based on time required to germinate up to 15 seeds, 1 being the fastest possible rate.

Species	Year and location collected	Site	Number of Replicates	TEMPERATURE							
				20°C		15°C		10°C		5°C	
				%	rate	%	rate	%	rate	%	rate
<i>Arctagrostis latifolia</i>	1971 Tuk	65 cutline	9	82 \pm 5	.41 \pm .04	87 \pm 3	.25 \pm .01	86 \pm 3	.21 \pm .01	80 \pm 5	.06 \pm .00
<i>Calamagrostis canadensis</i>	1970 Inuvik	Fireguard	4	81 \pm 4	.29 \pm .01	45 \pm 3	.19 \pm .01	28 \pm 5	.11 \pm .01	19 \pm 4	.06 \pm .00
<i>Festuca brachyphylla</i>	1972 Tuk	65 cutline	3	91 \pm 3	.07 \pm .00	93 \pm 1	.07 \pm .00	86 \pm 3	.04 \pm .00	8 \pm 3	
<i>Poa lanata</i>	1972 Tuk	65 cutline	3	99 \pm 1	.25 \pm .00	97 \pm 1	.19 \pm .00	96 \pm 2	.11 \pm .00	92 \pm 0	.05 \pm .00
<i>Festuca rubra</i> (Arctared)	1971 Agronomic		3	92 \pm 2	.33 \pm .00	88 \pm 2	.21 \pm .00	84 \pm 5	.14 \pm .00	56 \pm 6	.06 \pm .01
<i>Poa pratensis</i> (Nugget)	1971 Agronomic		2	92 \pm 4	.28 \pm .00	96 \pm 0	.22 \pm .01	86 \pm 6	.12 \pm .00	72 \pm 0	.05 \pm .00
<i>Eriophorum vaginatum</i>	1971 Tuk	Tussock Tundra	4	26 \pm 2	.10 \pm .00	0	0	0	0	0	0
<i>Carex Bigelowii</i>	1971 Tuk	Sedge-Cottongrass	3	3 \pm 1	-	-	-	-	-	-	-
<i>Betula nana</i> ssp. <i>erilis</i>	1971 Tuk	Shrub-Heath	3	25 \pm 2	.16 \pm .01	-	-	-	-	-	-

rate of germination at all temperatures, the most significant being at 10°C where it exhibited a rate nearly twice as high as all other species germinating 70% of its seeds in six days vs. only 25 to 40% for most other species.

Because of their mutual occurrence and importance in disturbed areas, but dissimilarity in both range and origin, *Arctagrostis* and *Calamagrostis* seeds were tested and compared over a range of temperatures between 5° and 35°C to determine the magnitude and direction of differences in temperature response. As can be seen from Fig. 5, the percent germination of *Arctagrostis* seeds is essentially unaffected by temperatures between 20° and 5°C, however, the rate of germination is fastest at 20°C (Fig. 6). At temperatures above 20°C both percent and rate of germination dropped, abruptly going to zero at 35°C. Optimum percentages and rates of germination for *Calamagrostis* occur between 25° and 30°C. Below 20°C both drop off rapidly, reaching lows at 5°C. Although the rate declined sharply above 30°C, germination remained relatively high ($70 \pm 4\%$).

Temperature Response as Affected by Microhabitat

In conjunction with the collection of environmental data in disturbed and undisturbed areas along the slope, seed heads of *Arctagrostis latifolia* were collected at each site near the end of August 1971. These were germinated along a temperature gradient and the data analysed to determine temperature, disturbance, and slope position effects on rate and completeness of germination (Table 15).

In all cases treatment effects were most clearly shown for seeds

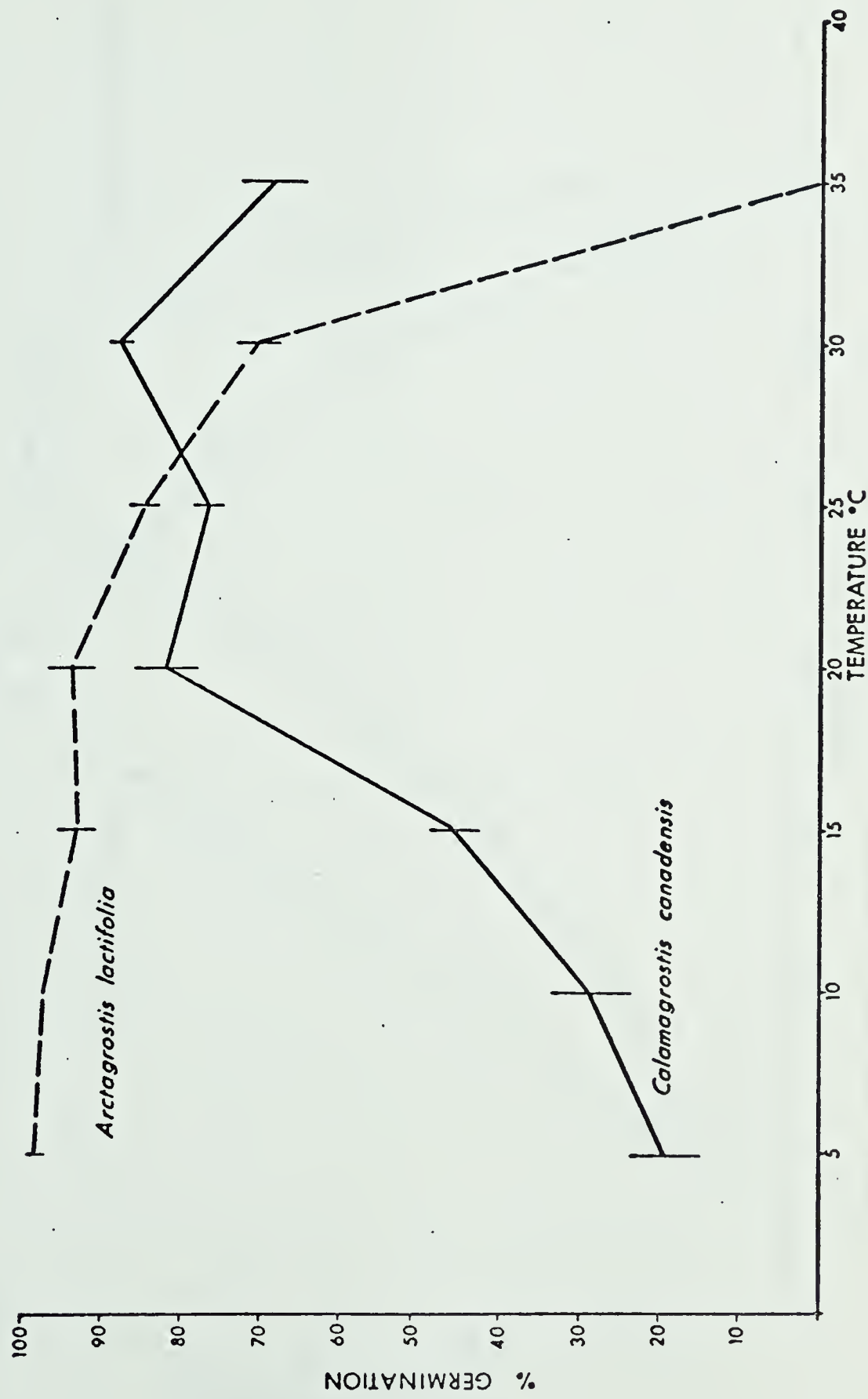


Figure 5. Mean \pm SE percent germination of *Arctagrostis latifolia* and *Calamagrostis canadensis* seeds as affected by temperature.

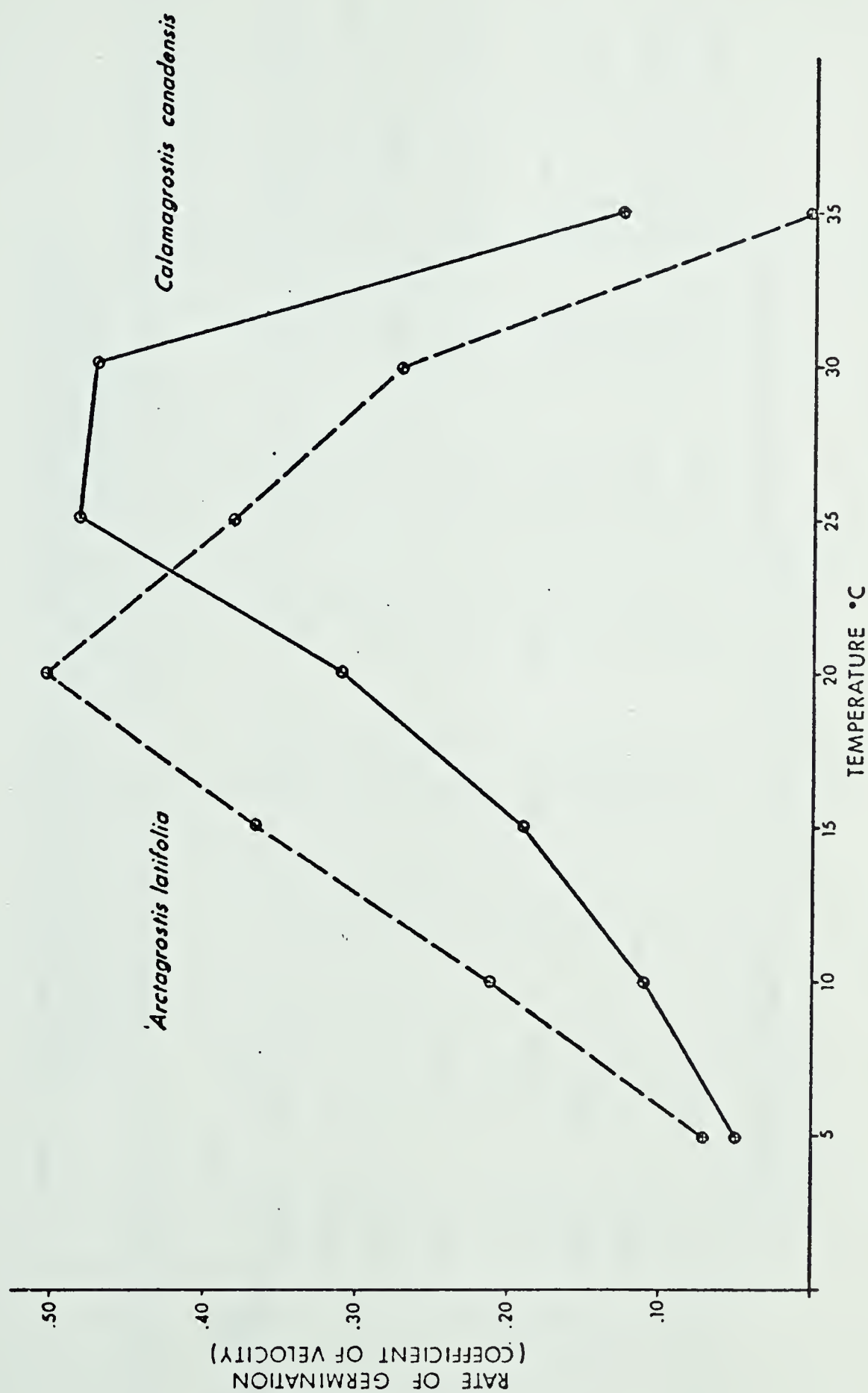


Figure 6. Mean rate of germination of *Arctagrostis latifolia* and *Calamagrostis canadensis* seeds as affected by temperature ($SE \leq \pm 0.03$). 1.0 is the fastest rate possible.

Table 15. Mean percent and rate of germination + SE of *Arctagrostis latifolia* seeds collected from top (1), mid (2) and bottom (3) slope positions in both disturbed (D) and adjacent undisturbed (N) sites and germinated along a temperature gradient from 5° - 20°C.

Location	Reps.	20°C						15°C						10°C						5°C					
		Σ		Rate		Σ		Rate		Σ		Rate		Σ		Rate		Σ		Rate		Σ		Rate	
D ₁	3	93 ± 3 aA	.50 ± .00 aA	92 ± 2 aA	.36 ± .01 aB	96 ± 0 aA	.24 ± .01 aC	97 ± 1 aA	.07 ± .00 aD	95 ± 1 a															
D ₂	3	86 ± 4 abA	.45 ± .04 abA	89 ± 1 aA	.27 ± .02 bB	88 ± 6 aA	.23 ± .02 aB	75 ± 3 bB	.06 ± .01 aC	84 ± 3 b															
D ₃	3	61 ± 13 bA	.29 ± .02 bA	80 ± 9 aA	.24 ± .01 bB	75 ± 1 bA	.16 ± .02 bC	68 ± 7 bA	.05 ± .00 bD	72 ± 6 c															
ND _{1,2,3}	9	82 ± 5 *	.41 ± .03 *	87 ± 3 *	.29 ± .02 *	86 ± 3 *	.20 ± .01 *	80 ± 5 *	.06 ± .00 *	84 ± 2 *															
N ₁	3	53 ± 18	.24 ± .03	54 ± 13	.21 ± .01	68 ± 7	.14 ± .01	35 ± 16	.04 ± .00	52 ± 7															
N ₂	3	70 ± 7	.34 ± .04	73 ± 18	.22 ± .03	61 ± 9	.11 ± .02	34 ± 8	.03 ± .00	59 ± 7															
N ₃	3	69 ± 5	.29 ± .02	80 ± 2	.24 ± .01	59 ± 15	.15 ± .03	57 ± 6	.05 ± .00	66 ± 6															
ND _{1,2,3}	9	64 ± 6 *	.29 ± .02 *	69 ± 8 *	.22 ± .01 *	63 ± 5 *	.13 ± .01 *	42 ± 7 *	.04 ± .00 *	59 ± 4 *															

* Data within a column having different small letters or within a row having different capital letters are significantly different according to Duncan's multiple range test.

* Data from the same column are significantly different at the 99% level.

collected from disturbed areas. Germination of seeds from undisturbed areas was quite variable which often masks treatment effects. This was possibly due to the much greater variability in microtopography and thus in active layer depth and soil temperature found in undisturbed areas vs. the more uniform disturbed areas.

Among slope positions, the effects of temperature on speed and completeness of germination are similar to those of previous tests. Temperature essentially has no effect on completeness of germination except at 5°C where percent germination usually decreases, especially in those seeds collected from undisturbed sites. In all cases germination rates were highest at 20°C and decreased with decreasing temperature, the greatest changes in rate taking place between 10° and 5°C.

Highly significant differences in germination occurred between seed from disturbed and undisturbed sites (Table 15). At all temperatures the completeness and speed of germination of seed from disturbed sites was greater than that from undisturbed sites. The mean difference in completeness of germination was 25% and, while rate differences varied with temperature, the greatest differences occurred at the higher temperatures.

Slope position effects were also significant but were only discernable in disturbed areas due to the high variability of germination in seed from undisturbed sites. At all temperatures, except 15°C, seeds from the hill-top position had a significantly more complete and faster rate of germination than those collected from the hill-bottom position.

Averaged over all temperatures, germination of seeds from the hill-top position was 11 and 23% greater than from the mid-slope and bottom slope position respectively.

Response to Moisture Stress

For plants in the Low Arctic, soil moisture is seldom a limiting factor (Dennis, 1969; Haag, 1974), although surface soils may dry considerably, especially in well-drained upland sites. Seeds, if they are to successfully germinate on these sites, must have the ability to do so under low to fluctuating water conditions or be prepared to lie dormant until sufficient moisture becomes available. The objective of this series of experiments was to determine the relative abilities of native and agronomic grass species to germinate under a range of moisture conditions.

All species showed at least a slight decrease in percent germination as water potential decreased (Table 16). *Poa lanata* and the agronomic *Festuca rubra* had the highest percent germination and the most consistently high rates of germination, being little affected by decreasing water potentials. Percent germination of *Arctagrostis* was significantly affected by each decrease in water potential while that of *Calamagrostis* showed no decrease until -6 bars. *Festuca brachyphylla* was the most dramatically affected by negative water potentials, ceasing to germinate at -3 bars.

Percent total germination (Table 16) was used as a measure of the ability of a species to experience drought conditions and then

Table 16. Mean percent and rates of germination (\pm SE) of selected species as affected by the water potential of the germination solution. Percent total germination represents that occurring after the solutions were rinsed off and distilled water was applied. All data are based on 3 replications of 25 seeds each.

Species	Year and Location Collected	Site	WATER POTENTIAL								
			Control			-3 Bars			-6 Bars		
			%	rate	%	%	rate	%	%	rate	%
<i>Arctostaphylos latifolia</i>	1972 Tuk	65 cutline	96 \pm 4	.35 \pm .01	67 \pm 6	.25 \pm .01	76 \pm 2	24 \pm 4	-	56 \pm 4	
<i>Calamagrostis canadensis</i>	1971 Inuvik	Fireguard	81 \pm 1	.23 \pm .00	76 \pm 6	.28 \pm .02	76 \pm 6	27 \pm 3	-	30 \pm 1	
<i>Poa lanata</i>	1972 Tuk	65 cutline	99 \pm 1	.25 \pm .00	95 \pm 5	.29 \pm .01	96 \pm 2	91 \pm 1	.28 \pm .01	97 \pm 2	
<i>Festuca brachyphylla</i>	1972 Tuk	65 cutline	91 \pm 3	.07 \pm .00	0	0	99 \pm 1	0	0	91 \pm 1	
<i>Festuca rubra</i> (Arctared)	1971 Agronomic		88 \pm 0	.35 \pm .00	89 \pm 6	.31 \pm .01	92 \pm 2	85 \pm 3	.28 \pm .00	92 \pm 2	

to germinate when adequate moisture becomes available. All species showed some ability to germinate after the drought treatment. The extent, however, was a function of how greatly seed germination had been retarded by the initial drought. *Poa lanata* and *Festuca rubra* were little affected by drought, and therefore showed only a slight increase in percent total vs. initial germination. *Arctagrostis latifolia* showed increases over initial germination at both -3 and -6 bars while *Calamagrostis canadensis* showed none. *Festuca brachyphylla* showed the most significant increases, increasing from zero germination at -3 and -6 bars to over 90% germination at 0 ψ .

Dark Germination

Seeds of *Arctagrostis latifolia*, *Calamagrostis canadensis* and *Eriophorum vaginatum*, tested in the dark at 20°C and with adequate moisture showed that germination was significantly reduced by darkness. The most significant reduction was that of *Eriophorum* which has a "dark" germination of only 4.4% of controls, followed by *Arctagrostis* with 68% and *Calamagrostis* with 69% of controls.

Summary and Discussion

The results of these tests suggest that germination is one of the key factors determining the species which will eventually become established in disturbed areas. All three species tested that are important in the native tundra have seeds with low percent and rates of germination at 20°C. Seeds of *Eriophorum vaginatum*, when tested at lower temperatures (\leq 15°C), do not germinate, and there is no reason

to suggest that the others would respond differently.

All species commonly found in disturbed areas have relatively high percent and rates of germination at all temperatures tested. Billings and Mooney (1968) reported that to the best of their knowledge, only one tundra species has been reported which could germinate at a continuous temperature of 5°C. In this study, all colonizing species tested were able to germinate at 5°C. *Arctagrostis latifolia* had one of the most complete and rapid germinations of all native species. Only *Poa lanata* had a higher percent germination, but its rate was consistently lower than that of *Arctagrostis*. The two agronomic species, *Festuca rubra* and *Poa pratensis*, also have high rates and percentages of germination, suggesting one of the reasons for their success in previous revegetation studies (Younkin, 1972). That they are able to do so well in arctic environments is not totally unexpected as *Festuca rubra* is a native species found throughout the Arctic, and *Poa pratensis* is an introduced species which already has acquired a circumpolar distribution (Hulten, 1968).

A comparison of germination characteristics of *Arctagrostis* and *Calamagrostis* seeds, suggests that speed and completeness of germination may be related to the range and origin of the species. *Arctagrostis*, a wide ranging arctic species with a narrow habitat preference, (see Chapters 2 and 3), has the highest rates and most complete germination at temperatures below 20°C with a very abrupt germination cut off at 35°C. *Calamagrostis*, a species ranging from arctic to temperate regions has seeds with rates and percent germination above 20°C and little

reduction in germination at 35°C. Although significantly reduced, some germination occurs at 5°C.

Germination tests of seeds from populations of *Arctagrostis* plants growing in different microhabitats shows that both disturbance and slope position can have a significant effect on germination. The speed and completeness of germination was greater in seeds from disturbed than undisturbed sites, with seeds from the disturbed hill-top and mid-slope positions having faster and more complete germination than those from the hill-bottom position. This is possibly related to the increased vigor and nutrient contents observed in plants found in disturbed upland sites which in turn may be related to the warmer and deeper active layers found at these positions (see Chapter 5).

Under conditions of increasing aridity, many of the native species tested showed a separation of germination ability along habitat lines. *Poa lanata*, a common species in well-drained undisturbed and disturbed sites, has seeds essentially unaffected by aridity, maintaining a complete and rapid germination under all conditions tested. Another species more common in drier areas, *Festuca brachyphylla*, has seeds which do not germinate at all under water stress. However, when fresh water was added over 90% of the seeds germinated, suggesting that they can survive periods of drought and still remain viable. *Arctagrostis latifolia*, generally found in moist to mesic sites, has seeds which decline in percent germination as water stress increases. More than 50% of the seeds still germinate after removal of the water stress. *Calamagrostis canadensis*, which tolerates a wider range of habitats than does *Arctagrostis*, has seeds less affected by aridity, and, in

fact, the rate of germination appears to be stimulated by an increase in water stress up to -3 bars. At -6 bars, percent germination decreases considerably, and recovery after this stress is poor.

If a species is to become a colonizer of disturbed areas, it must first have a nearby seed source and/or good dispersal mechanism and also be able to germinate in the provided habitat. Although many of the important tundra species do provide a large and nearby seed source, the results of the germination experiments suggest that they are not able to satisfy the second criterion. In contrast, species commonly important in disturbed areas are not of great importance in the native tundra. However, they do provide a viable seed source which will germinate under a wide range of environmental conditions. It would seem that these latter species are ecological opportunists; not really well adapted to the closed tundra situation but having the ability to survive by producing viable seeds until some type of disturbance provides a suitable habitat.

CHAPTER VII

PLANT GROWTH IN COLD SOILS

The presence of permafrost constitutes one of the most unique features of the arctic tundra, creating environmental conditions which are seldom encountered in areas further south. Formed before the end of the last glaciation, the continuous permafrost zone in North America today extends north of latitude 67° which approximates the southern boundary of tundra vegetation (Mackay, *et al.*, 1972). Though permafrost was originally formed under a past cooler climate (Terasmae, 1973), the present climate in the Low Arctic is cool enough that, in conjunction with an insulating layer of organic matter and vegetation, permafrost is maintained and in certain areas continues to grow (Mackay, *et al.*, 1972).

During the growing season air temperatures on the Tuktoyaktuk Peninsula are surprisingly high, with daily mean and mean maxima in July being 10 and 15°C respectively and in August 9 and 12°C respectively (AES, 1972). Within the vegetation boundary layer, air temperatures are even warmer, daily mean and mean maxima in July being 13 and 20°C respectively and in August 10 and 16°C (1972 field data). Although the relatively warm growing season is short in comparison to temperate regions (8 to 10 weeks in the Low Arctic compared to 14 to 16 weeks in north temperate areas) this is partially compensated for by continuous daylight much of this period.

In the shallow active layer lying just above the permanently frozen soil, the growing season environment is much cooler. Soil temperatures in the upper 10 to 15 cm seldom rise above 7°C and more frequently lie between 3 and 4°C (Bliss, 1956; Kelley and Weaver, 1969; Younkin, Chapter 4). It is here that over 80% of the plant's total biomass resides in the form of roots and rhizomes (Dennis and Johnson, 1970) functioning both in food storage and in water and nutrient uptake (Billings, 1973).

How cold soil affects plant growth is not completely understood. It is believed to directly affect plants in terms of water and mineral uptake (Kramer, 1940; Zhurbitsky and Shtrausberg, 1958), and in mineral incorporation (Dadykin, 1958; Korovin, *et al.*, 1963), and indirectly by limiting the rate of microbial release of nutrients to the soil (Douglas and Tedrow, 1959).

Studies of decomposition in a number of tundra soils (Douglas and Tedrow, 1959) reveal that the total annual decomposition in the Arctic is low ranging from 600 to 1700 kg/hectare vs. 3000 to 4000 kg/hectare in temperate areas (Alexander, 1961). The rate of decomposition was shown to be strongly temperature limited, a decrease in temperature from 19°C to 7°C resulting in an 80% reduction in rate. Haag (1972) working in a low shrub-heath community on the Tuktoyaktuk Peninsula calculated that decomposition would add only 99 kg of nitrogen and 10 kg of phosphorus per hectare per year. However, Warren Wilson (1966) in a comparison of fertility between soils from Great Britain and Cornwallis

Island in the High Arctic concluded that soil fertility alone could not account for the low production in arctic regions.

The concept of the physiological aridity of cold soils, originally proposed by Sachs (Dadykin, 1958), has been demonstrated for a number of temperate species (Kramer, 1940, 1942). Studies by Kramer (1940) have suggested that the water stress observed in plants at low root temperatures is due not so much to a decrease in root respiration as to an increase in protoplasm and water viscosity, both of which decrease the rate of water uptake. The use of this concept in explaining the low production of arctic plants has been criticized by Dadykin (1950, 1958) who contended that transpiration rates of many arctic plants are not much lower than those of many temperate region species and pointed out that the application of this theory to arctic areas ignores the concept of the formative role the environment plays in the adaptation of an organism to its environment. Current field studies have reported relatively low water potentials in tissues of plants growing in cold soils (Haag, 1972; Teeri, 1973; Courtin and Addison, 1972; Younkin, Chapter 4), however, little has been done on an experimental basis to determine the effects of soil temperature on the water balance in arctic species.

Studies of a number of field crops have demonstrated that the uptake and assimilation of both phosphorus and nitrogen are limited by low root temperatures (Shtrausberg, 1958, Dadykin, 1958; Korovin *et al.*, 1963). Both elements are of major importance to the plant and both are in relatively low supply in tundra soils (Janz, 1974).

Though nitrogen has often been identified as a limiting factor in arctic regions (Haag, 1972; Warren Wilson, 1959; Sorensen, 1941; Russell, 1940), the interaction of both elements in various plant processes is so complex and interrelated that it can be misleading to stress the importance of one over the other (Korovin *et al.*, 1963; Savile, 1972). While Dadykin (1958) has stressed the influence of low root temperatures in reducing nitrogen assimilation, Korovin *et al.*, (1963) have pointed out that the reduction of phosphorus uptake and assimilation at low temperatures, affects not only glycolysis and respiration but also decreases the formation of high energy phosphate bonds important to many energy requiring processes including nitrogen metabolism.

Though research has been conducted into the factors limiting photosynthesis in arctic species (Warren Wilson, 1966; Tieszen, 1973) and models have been proposed integrating the factors believed to be controlling primary production in arctic regions (Tieszen, 1973; Whitfield, 1972) little consideration has been given to the influence of cold soils. Tieszen (1973) studying the photosynthetic responses in a number of arctic grasses to different radiation and temperature regimes identified radiation as the most effective in controlling the rate of photosynthesis. Warren Wilson (1966) has proposed feedback inhibition of photosynthesis by accumulated photosynthates as an explanation of the low growth in arctic regions. In his hypothesis, low air temperatures depress respiration and assimilation of photosynthates. Though not stated as such, it is possible to visualize the accumulation of photosynthates in above ground parts due to the influence of cold soils in preventing their rapid incorporation into root reserves. This has been suggested as

a factor in the reduction of photosynthesis and the formation of anthocyanins prior to dormancy in certain alpine plants (Spomer and Salisbury, 1968). In a recent study of the influences of cold soils on growth and various physiological processes of alpine plants, Anderson and McNaughton (1973) found that though growth was considerably reduced at soil temperatures of 3°C vs. 20°C, there was no reduction in the rate of photosynthesis. Decreased root growth and metabolism at low soil temperatures was suggested as one possible cause of the reduced plant growth.

Though much of the evidence suggests that the reduction in growth of plants growing in cold soils is related to mineral nutrition, how plants have adapted to this is not clear. It has been suggested that it may be due to the evolution of enzyme systems capable of efficiently extracting nutrients at low temperatures or a more efficient utilization of available and incorporated nutrients (Savile, 1972). Loveless (1961) presents evidence that a morphological adaptation to low soil phosphorus in tropical areas is the development of sclerophylly while Clarkson (1967) from studies of several species of *Agrostis* growing on low phosphorus soils has suggested an ability to tolerate low growth rates. Chapin (1972) from his studies of phosphorus uptake by *Eriophorum vaginatum* presents evidence which suggests that it is not so much a more efficient nutrient utilization as it is the ability to produce larger amounts of nutrient absorbing root biomass at low temperatures. This is also suggested from observations by Dadykin (1958) and Tyrtikov (1964) that plant responses to low soil temperature results in thickening, reduction in ramification and increases in root weight.

The objectives of the present research were to measure and compare the effects of low soil temperatures and low soil nutrient content on growth and development, tissue nutrient contents, leaf water potentials and rates of photosynthesis of two arctic grasses *Arctagrostis latifolia* and *Calamagrostis canadensis*.

Methods

To meet the above objectives an experiment was designed utilizing the controlled environment facilities at the University of Alberta. The general procedure in this experiment was to grow both grasses in fertilized and unfertilized arctic soils obtained from a 1965 seismic line. Half of the pots from each group were placed in a growth chamber where soil and air temperatures were maintained at 15°C. The other half were placed in the same growth chamber on a specially designed soil cooler (called a permafrost simulator) which allowed soil temperatures to assume a gradient similar to that found in permafrost regions while surface and air temperatures were maintained at 15°C. Various measurements, described below, were made and the statistical significance of treatment effects determined. The following is a detailed description of the various aspects of the methods.

Soil and Pot Preparation

The soil used throughout the experiment was a sandy clay loam (51% sand, 15% silt, 34% clay, pH 4.5) removed from the upper 15 to 20 cm of the 1965 seismic line near Camp Waltrus. The soil was stored air dry in a freezer until use at which time it was shredded and sieved.

A desorption curve was developed from pressure plate analysis at $-1/3$, -3 and -15 bars.

Twenty 15 cm plastic pots were filled with 1772 g of this soil for each species. A nutrient treatment of N, P and K at the rate of 50, 50 and 100 ppm respectively was added to the bottom 800 g of soil in half of the pots. Amonium nitrate ($\text{NH}_4 \text{NO}_3$) was used to provide nitrogen, and potassium phosphate (K_2HPO_4) the potassium and phosphorus. Both fertilizers were ground to a fine dust and aliquots randomly selected and weighed. The amounts for each 800 g of soil were added to 25 ml of distilled water and sprinkled onto the soil as it was being mixed on a plastic sheet. Placement of the fertilizer into the bottom half of the pot was to insure that the root systems of plants growing in those soils on the soil cooler would have to extend into a zone cooler than 5°C to take advantage of the added nutrients.

Permafrost Simulator: Design and Operation

The soil cooling device used to simulate permafrost conditions was a rectangular galvanized iron tank (120 cm X 90 cm X 20 cm) containing refrigerator coils and a circulating pump and filled with ethylene glycol (Fig. 7). A thermostat control allowed the selection of the desired solution temperature. Ten pots of each species, five fertilized and five unfertilized, were placed directly on the tank. A styrofoam lid with holes cut for each pot was fitted around the pots (Fig. 8). This exposed the soil surfaces and grass shoots to air temperatures but insulated the rest of the pot and soils establishing a gradient of soil temperatures.

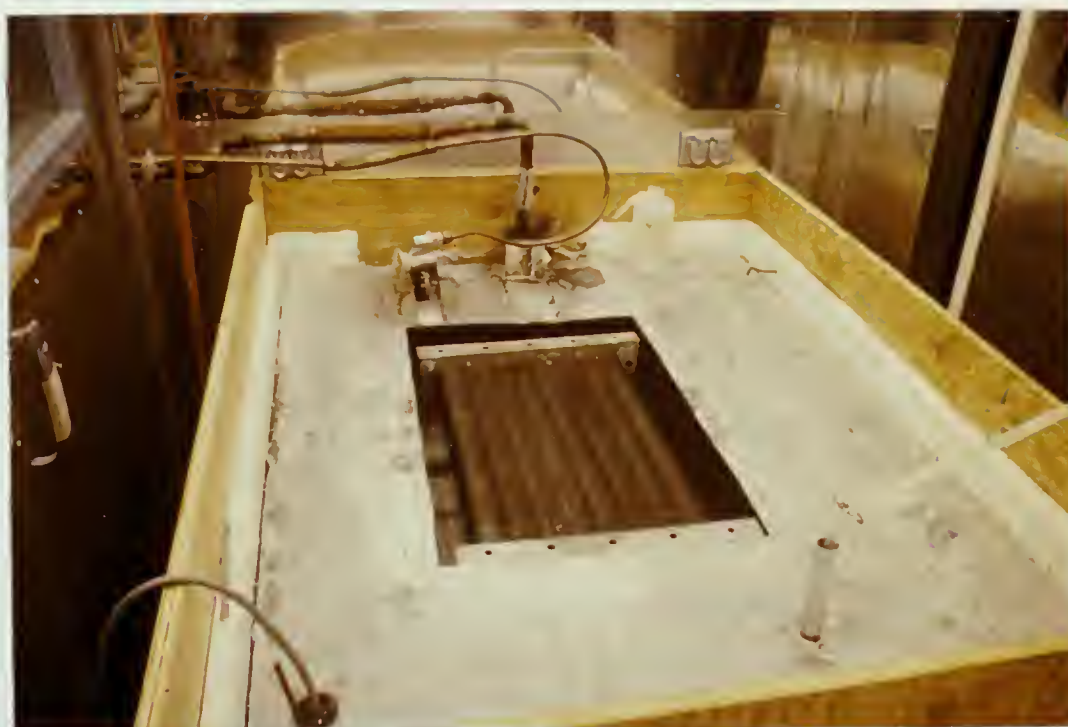


Figure 7. Permafrost simulator with inspection plate removed showing refrigerator coils immersed in ethylene glycol solution.



Figure 8. Permafrost simulator during operation.

Soil temperature measurements taken in 1972 on the Tuktoyaktuk Peninsula provided an accurate basis for temperature simulation during this experiment. An average soil temperature gradient in July in an undisturbed hummock was 6 to 8° at -10 cm, 3.5 to 5.5° at -20 cm and 1.5 to 2°C at -30 cm. The gradient established on the soil cooler in 14 cm of soil was $7.5^{\circ}\pm 1$ at -2 cm, $4^{\circ}\pm 1$ at -7 cm and $2^{\circ}\pm 1$ at -12 cm. The gradient was much steeper than found under natural conditions but was necessary to simulate conditions of a 30 cm active layer in a 14 cm pot. Thermocouples connected to a 24 point recorder (Honeywell Electronic 16) were placed in several of the pots and monitored regularly for a 24 hr period to determine stability of the temperature gradient.

Operating Conditions

The entire experiment was set up in an M-12 Environmental Growth Chamber. Lighting, a mixture of fluorescent (90% lumens) and incandescent lamps, (10% lumens) was continuous. Air temperature was maintained at a constant $15^{\circ}\pm 0.5^{\circ}\text{C}$ with a relative humidity between 45 to 60% . Using soil desorption curve data, the soils in each pot were maintained at field capacity throughout the experiment. Pot positions were systematically changed daily to minimize the effects of environmental differences within the chamber. The pots were labeled according to the treatment received; C = *Calamagrostis*, A = *Arctagrostis*, P = permafrost simulation (8 to 0°C), F = added fertility. C or A alone indicates that those species were grown in unchilled (15°C), unfertilized soils, the addition of the other letters indicating a variation of this condition.

Data Collection and Measurements

Growth and Production

The length of the longest leaf and the number of shoots per plant were recorded at weekly intervals throughout the experiment. At the end of the eighth week the above-ground parts of each plant was harvested, dried at 80°C for 24 hr and weighed. All pots were then frozen, the soils removed intact and cut in half horizontally with a hacksaw. For those pots removed from the soil cooler, the 0 to 7 cm section represented the soil temperature gradient from 8 to 4°C while the 7 to 14 cm section represented the gradient from 4 to 1°C. The soils were then allowed to thaw and each half was carefully washed and sieved to remove all roots. Roots were dried at 80°C for 24 hr and weighed. Tissue samples of both leaves and roots were ground in a Wiley mill and sent to the Alberta Soil and Feed Testing Laboratory where they were analyzed for N, P and K. Nitrogen was determined by the macro Kjeldahl method, phosphorus by the vanado-molybdate method and potassium with a flame photometer.

Water Potential

Leaf water potential measurements were made at the end of the seventh week of growth using a water bath thermocouple psychrometer. Replicate measurements of leaves of both species at all treatment conditions were made. Lower leaves from the youngest shoots were selected, clipped at the base of the sheath and placed directly into the psychrometer. These were placed into a constant temperature water bath and allowed an equilibrium time of three hours. The thermocouple cooling period (4 ma) was ten seconds, the microvolt reading being made with a Fluke

model 845 A-B microvoltmeter. Microvolt readings were converted to water potentials in bars using calibration curves developed for each psychrometer.

CO₂ Gas Analysis

Pots of *Arctagrostis* plants grown both in cooled and uncooled soils and a pot of *Calamagrostis* plants grown in uncooled soils were placed in a nearby growth chamber equipped for CO₂ analysis during the seventh week of the experiment. Here the effects of soil temperature on *Arctagrostis* and the effects of light intensity on both *Arctagrostis* and *Calamagrostis* were measured using CO₂ analysis.

The light source for the experiment was a combination of inflourescent and incandescent lamps. The intensity was varied both by varying the intensity of the source and by using cheesecloth filters. Intensity measurements were made with a Lambda model LI-185 Quantum/Radiometer/Photometer. Soils were cooled with a Peltier cooling block. A single pot was placed within an insulated aluminum container which was then placed on the Peltier cooling block. Soil temperatures were measured with copper constantan thermocouples implanted at -4 and -8 cm. Air temperature within the chamber was maintained at 15⁰-0.5C. Leaves of selected plants were placed within a 22.8 X 15.2 X 1.9 cm curvette made of Plexiglass. Leaf temperatures were measured with a fine wire copper constantan thermocouple and were never more than 1⁰C above ambient. A 0.5 to 2 hr pretreatment at each light and temperature combination was given before the analysis.

Carbon dioxide exchange was measured with a MSA LIRA 200 infrared gas analyser. An open system was used, ambient air being pumped from outside the building into a large mixing tank to damp CO₂ fluctuations. The measured flow rate through the chamber was 385 ml/min. Air leaving the chamber was dried, analysed for CO₂ and exhausted. Air from the cuvette was analysed for 20 min and ambient air for 15 min. At the end of the experiment the leaves within the cuvette were clipped, dried and weighed.

Data Analyses

Data analyses were accomplished using both F and Student t-tests (Steel and Torrie, 1960). The shoot and root production experiment was analysed as a 2 x 2 factorial with two levels of soil temperature and two levels of fertility as the factors. To eliminate the effects of any inherent size differences between species, comparisons of species effects were made using the ratio of change between control and treatment conditions. Plants growing in warm, nutrient poor soils were arbitrarily selected as controls.

Results

Growth and Morphology

Leaf lengths and leafy stem numbers were significantly affected by nutrient and temperature treatments (Table 17). Both were lowest in cold low nutrient soils and greatest in warm high nutrient soils. Under all treatments *Arctagrostis* produced longer leaves but fewer leafy stems than *Calamagrostis*. Applications of nutrients counteracted

Table 17. Mean \pm SE of leaf length (cm) and stem numbers of *Arctagrostis* and *Calamagrostis* plants grown under various soil temperatures and nutrient levels. Data followed by the same capital letter are significantly different at the 95% level and represent the date of the first significant difference between plants grown in fertilized and unfertilized soils.

Days From Start of Experiment	Leaf Lengths (cm)										Stem No.
	12	21	28	35	42	49	56	63	70	70	
15°C											
Arctagrostis	4.6 \pm .2	9.3 \pm .4	16.0 \pm .8	20.9 \pm .9	24.7 \pm 1.8	26.1 \pm 1.1	27.4 \pm 1.2	29.4 \pm 1.3	30.0 \pm 1.3	2.8 \pm .2	
Calamagrostis	4.1 \pm .2	8.3 \pm .4	13.2 \pm .7	16.7 \pm .7 A	20.9 \pm .5	22.9 \pm .5	23.9 \pm .6	24.8 \pm .6	25.8 \pm .7	7.1 \pm .4	
8-0°C											
Arctagrostis	4.8 \pm .3	7.3 \pm .4	11.0 \pm .5	14.5 \pm .7	18.2 \pm .8 C	18.9 \pm .8	19.3 \pm .8	19.7 \pm .8	20.0 \pm 1	1.6 \pm .2	
Calamagrostis	4.0 \pm .2	6.3 \pm .4	8.1 \pm .5	10.0 \pm .5	12.6 \pm .5	14.0 \pm .4 D	14.6 \pm .7	15.4 \pm .7	16.4 \pm .7	3.5 \pm .2	
15°C											
Arctagrostis	4.5 \pm .2	8.5 \pm .5	15.9 \pm .8	23.1 \pm .9	28.4 \pm 1.8	33.2 \pm 1.5	37.0 \pm 1.8	41.0 \pm 1.8	42.4 \pm 1.9	3.4 \pm .2	
Calamagrostis	3.9 \pm .2	7.9 \pm .5	14.9 \pm .8	19.9 \pm .7 A	24.6 \pm .6	27.7 \pm .8	29.5 \pm .9	32.8 \pm .9	34.5 \pm 1	9.4 \pm .8	
8-0°C											
Arctagrostis	4.8 \pm .3	7.2 \pm .4	11.7 \pm .8	16.8 \pm .9	22.3 \pm 1.2 C	24.3 \pm 1.3	25.0 \pm 1.4	27.4 \pm 1.6	29.4 \pm 1.7	1.9 \pm .2	
Calamagrostis	3.6 \pm .2	5.2 \pm .3	7.2 \pm .4	9.9 \pm .4	13.4 \pm .5	16.4 \pm .6 D	20.0 \pm .6	20.7 \pm .6	21.4 \pm .6	3.5 \pm .4	

the effect of cold soils, encouraging the production of leaf lengths similar to those produced on warm low nutrient soils, although the number of shoots remained unchanged. In general, nutrients had the greater influence on leaf lengths while soil temperature had the greater influence on the number of shoots produced.

By comparing leaf length of plants grown on fertilized and unfertilized soils over the duration of the experiment it was possible to determine when root systems had reached the nutrient rich zone. *Calamagrostis* plants growing in warm fertilized soils showed significant leaf increases over plants growing in warm unfertilized soils 35 days from the start of the experiment. *Arctagrostis* plants growing on both warm and cold soils showed a significant increase 42 days from the start of the experiment, however, *Calamagrostis* plants growing on cold soils did not show any significant increase until the 49th day.

Root and Shoot Weights

Treatment Effects. Statistical analyses (Table 18) revealed that in almost all cases soil temperature and soil fertility have a significant effect on root and shoot production and that there was significant interaction. Fertilized plants grown in warm soils had the greatest and unfertilized plants grown in cold soils the least above and below ground production (Table 19). A comparison of the simple effects of either treatment showed that both have approximately equal effects on shoot production, low soil temperature or low nutrients resulting in 50 to 65% reductions.

Table 18. Results of 2 x 2 factorials on the effects of soil temperature and fertility on root and shoot growth of *Arctagrostis* and *Calamagrostis*.

		Mean Square			
Source of Variation	D.F.	<u>Root Weight (mg)</u>		<u>Shoot Weight (mg)</u>	
		<i>Arctagrostis</i> Depth (cm)		<i>Calamagrostis</i> Depth (cm)	
		0 to 7	7 to 14	0 to 7	7 to 14
Temperature (T)	1	.042	1.198*	.341*	.777*
					1.52*
					2.98*
Soil fertility (S)	1	.764*	0.23*	.527*	.056*
					2.23*
					2.93*
T X S	1	.007	.119*	.063*	.037*
					.194*
					0.99*

* significant at the 1% level.

Treatment effects on root production varied between species. In the upper 7 cm section of the pot (8 to 5°C zone in cooled pots) soil temperature had no significant effect on root production of *Arctagrostis* though low soil fertility reduced production 46 to 48%. In the 7 to 14 cm section of the pot (5 to 0°C zone in cooled pots) *Arctagrostis* root production was reduced 84 to 86% by low soil temperature but only 49 to 53% by low nutrients. *Calamagrostis* root production was significantly effected by temperature and fertility in both soil zones, low temperature and low fertility having nearly equal effects in the upper 7 cm (41 to 47% reductions) while in the 7 to 14 cm section cold soils resulted in reductions of 92 to 94% and nutrients 37 to 50%. The addition of soil nutrients counteracted the effects of low soil temperature for the shoot systems and the 0 to 7 cm section of the root systems i.e. for shoots A=612 mg, AP=257 mg and APF=728 mg. Although the root systems in the 7 to 14 cm zone were stimulated by additions of nutrients (i.e. A=390 mg, AP=56 mg and APF=119 mg), it was not enough to overcome the effects of low soil temperature.

Species Response. To make valid comparisons of the response of to a particular treatment it was necessary to eliminate inherent differences due to genetic makeup. In this section all growth responses to treatments are expressed as percent changes from the growth response when grown in warm low nutrient soils. Under no treatment conditions was there a significant difference between species in shoot production (Table 20) although *Calamagrostis* responded more to a warm high nutrient soil (190% increase vs. 141% increase for *Arctagrostis*) but less than

Arctagrostis to a cold high nutrient soil (-1% vs. +19%) (Table 21). *Arctagrostis* produced larger total root masses under all treatments except warm nutrient rich soils, the largest differences occurring in the upper 7 cm (8 to 5°C) section of fertilized and unfertilized cold treated pots. In unfertilized cold soils *Arctagrostis* root production was only reduced 11% compared to 41% for *Calamagrostis*. With the addition of nutrients *Arctagrostis* root production surpassed that of the controls by 64% vs. 5% for *Calamagrostis*.

Though smaller, the differences in root production between species at the lower 7 cm section of the pots were highly significant. On warm low nutrient soils the addition of nutrients stimulated a 96% increase in root production for *Arctagrostis* vs. only a 5% increase for *Calamagrostis*. Under low nutrient, low temperature (5°C to 0°C) conditions, *Arctagrostis* roots were reduced 86% compared to 94% for *Calamagrostis*. The addition of nutrients to the cold soils resulted in a greater stimulation of *Arctagrostis* roots, their reduction below controls being only 69% vs. 88% for *Calamagrostis*.

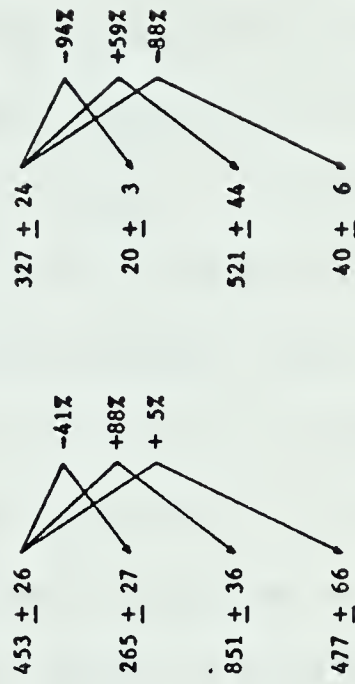
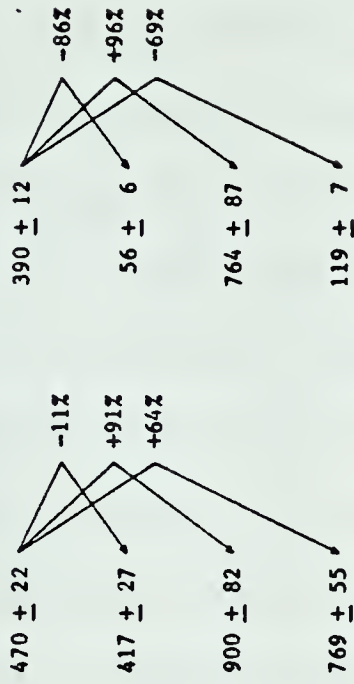
Differences in the response of species to temperature and fertility treatments resulted in significant differences in root:shoot ratios (Table 20). Under all treatments *Arctagrostis* had root:shoot ratios of greater than one while *Calamagrostis*, except for plants grown on warm low nutrient soils, had ratios lower than one (Table 21). The greatest differences between species occurred on cold nutrient deficient soils where *Arctagrostis* produced a ratio twice that of *Calamagrostis*. The lowest ratios for both species occurred on warm high nutrient soils.

Table 20. Values of "t" for unpaired t tests comparing differences in treatment effects on shoot and root production of *Arctagrostis latifolia* and *Calamagrostis canadensis*. Tests of significance for root/shoot ratios were based on absolute weights while all others were based on changes in weight from controls (15°C, unfertilized).

Soil Treatment	Shoot Wt (mg)		Root Wt (mg)		Root/Shoot Ratio	
	Total		0 to 8	8 to 14 cm	Total	Ratio
15°C, unfertilized (A vs C)	0.49		1.63	2.29*	3.39*	3.7**
8°C to 0°C, unfertilized (AP vs CP)	1.13		2.41*	3.89**	2.24*	5.27**
15°C, fertilized (AF vs CF)	1.67		1.72	1.39	0.40	3.73**
8°C to 0°C, fertilized (AFP vs CFP)	1.48		3.09*	6.17**	2.80*	3.54*
* Significant at the 5% level		A = <i>Arctagrostis</i>		P = Permafrost simulation		
** Significant at the 1% level		C = <i>Calamagrostis</i>		F = Added soil fertility		

Table 21. Mean \pm SE of shoot and root production, root:shoot ratios and mean percent changes (+,-) in production from controls (15°C, unfertilized) of *Arctagrostis latifolia* and *Calamagrostis canadensis* under various soil temperature and fertility treatments.

Species	Soil Treatment	Root:Shoot Ratio	Shoots (mg)	Roots (mg)	0-8 cm	8-14 cm
<i>Arctagrostis latifolia</i>	15°C, unfertilized	1.4	612 \pm 31	470 \pm 22	390 \pm 12	
	8° to 0°C, unfertilized	1.8	257 \pm 23	417 \pm 27	56 \pm 6	
	15°C, fertilized	1.1	1478 \pm 101	900 \pm 82	764 \pm 87	
	8° to 0°C, fertilized	1.2	728 \pm 53	769 \pm 55	119 \pm 7	
<i>Calamagrostis canadensis</i>	15°C, unfertilized	1.2	638 \pm 48	453 \pm 26	327 \pm 24	
	8° to 0°C, unfertilized	.9	313 \pm 30	265 \pm 27	20 \pm 3	
	15°C, fertilized	.7	1851 \pm 153	851 \pm 36	521 \pm 44	
	8° to 0°C, fertilized	.8	631 \pm 65	477 \pm 66	40 \pm 6	



Leaf Water Potentials

Mean water potential readings for *Calamagrostis* were consistently lower than those of *Arctagrostis* with significant differences occurring under control and cold high nutrient conditions (Table 22). Low soil temperature resulted in significant decreases in leaf ψ for *Arctagrostis* but not for *Calamagrostis*. When compared over all treatments leaf ψ of *Arctagrostis* plants grown in cold soils was an average 3 bars lower than that of plants grown in warm soils (-9.4 vs. -6.1). In comparison to controls, *Arctagrostis* plants grown in warm high nutrient soils showed an increase in water potential while those grown in cold low nutrient soils showed a decrease. *Calamagrostis* plants showed no significant difference from controls under any of the treatments. This may be partially a result of the high variability of readings observed within sampled populations of both species, masking all but highly significant treatment effects.

Table 22. Means + SE of leaf water potentials of *Arctagrostis latifolia* and *Calamagrostis canadensis* grown under various soil temperature and fertility treatments.

Species	15°C unfertilized (control)	15°C fertilized	8 to 0°C unfertilized	8 to 0°C fertilized
<i>Arctagrostis latifolia</i>	- 7.2+ .8	*-3.7+1.2	*-10.8+1.4	-6.8+1.5
<i>Calamagrostis canadensis</i>	-11.6+1.9	-7.3+1.8	-12.2+ .5	-13.7+1.5

* Significantly different from controls (15°C, unfertilized) at the 5% level.

CO₂ Exchange

Individuals of both species tested were grown at low soil temperatures, the objective being to observe how plants acclimated to low temperatures responded to changes in light intensity and soil temperature. Soil temperatures were maintained between 6 and 10°C during light intensity treatments. Determination of soil temperature effects on photosynthesis was made by allowing soils to warm to 12°C and then recording CO₂ assimilation changes as they were cooled to 3 to 4°C over a 12 hr period.

Both species maintained relatively high photosynthetic rates under low light intensities (Fig. 9). *Arctagrostis* had higher fixation rates at the lower light intensities and maintained a positive rate at light intensities as low as 40 lux and a higher rate than *Calamagrostis* up to 4500 lux. Above 4500 lux *Calamagrostis* had the more positive rate, increasing rapidly up to 9500 lux while that of *Arctagrostis* appeared to level off.

Arctagrostis was the only species tested in relation to soil temperature changes. There were no significant changes in rate of CO₂ fixation until temperatures were lowered to between 5 to 6°C (Table 23). At 3°C the rate of fixation dropped off to 12.7 mg CO₂/hr./g dry wt, a drop of approximately 24% from the high of 16.74 at 15°C. Because of limitations in the cooling method it was not possible to hold this lower temperature for more than one hour and it is not known if the plant would have acclimated and increased its rate of fixation.

Figure 9. Net photosynthesis of *Arctagrostis latifolia* and
Calamagrostis canadensis in relation to light intensity
at an air temperature of 20°C and mean soil temperature
of 8°C.

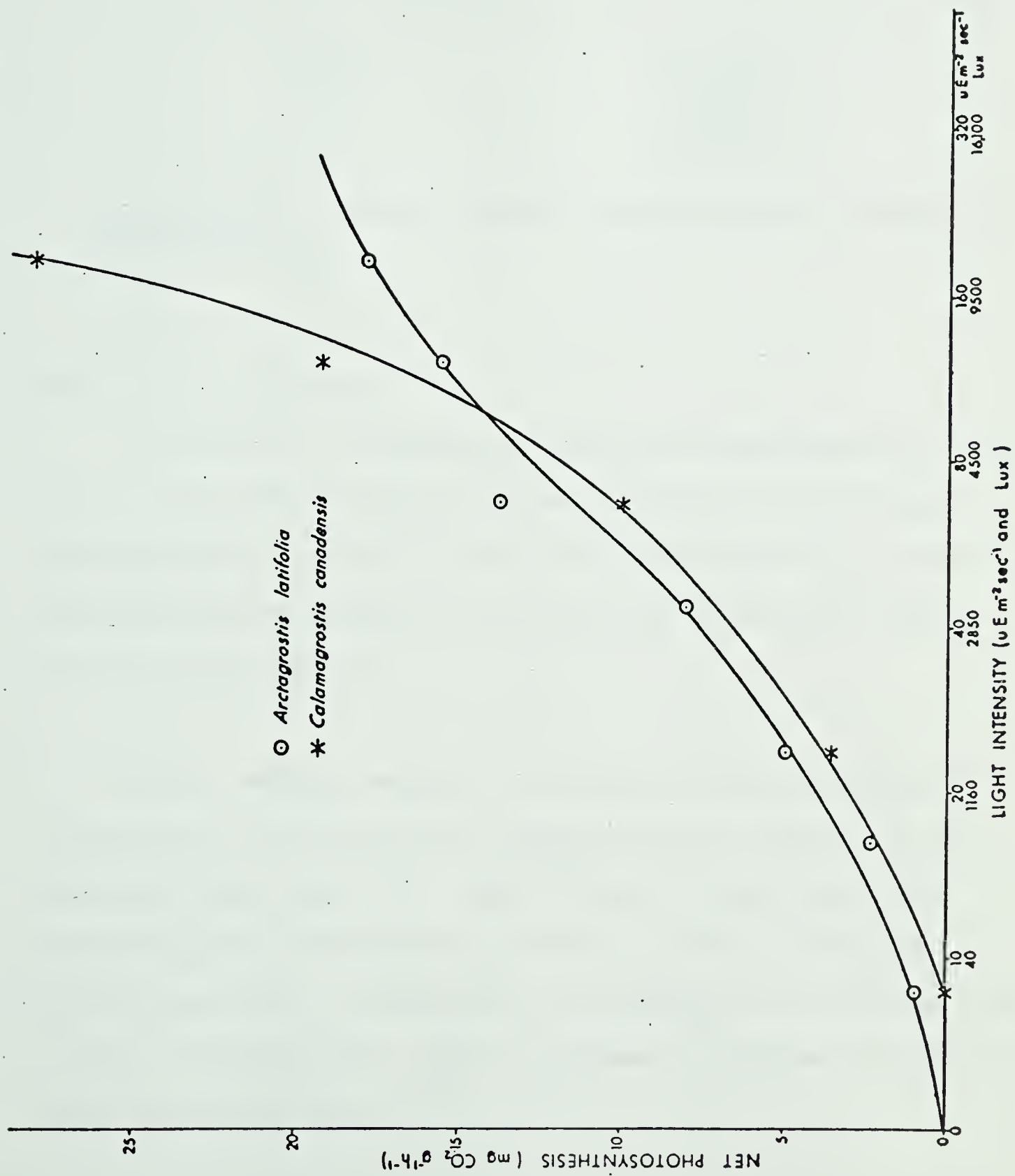


Table 23. Mean + SE net assimilation rates of *Arctagrostis latifolia* in relation to soil temperature. Means are based on 2 to 4 consecutive replicates in time.

Soil Temperature (°C)	Net Assimilation
11-12	16.74+.29 a*
9-10	16.63+.66 a
7- 8	16.19+.58 a
5- 6	14.81+.21 b
3- 4	12.72+.35 c

* Readings with a different subscript are significantly different at the 95% level.

Tissue Nutrient Analysis

In addition to the percent nutrient content measurements provided by the soil and feed testing laboratory, nutrient totals per plant and mg nutrient accumulation per mg root at the end of the experiment were calculated to emphasize the influence of the treatment effects on nutrient accumulation.

Nutrient analyses revealed that percent nitrogen was higher in plants grown in cold soils, the greatest increases occurring on the fertilized soils (Table 24). Total nitrogen per plant was similar for both species with decreases of from 35 to 45% for those plants grown on cold soils. Accumulation of nitrogen per mg of root was consistently greater for *Calamagrostis* than for *Arctagrostis*, the greatest differences occurring on cold soils.

Table 24. Percent and total nutrient contents and mg nutrient accumulation per mg root for *Arctagrostis* and *Calamagrostis* plants grown under various soil temperature and nutrient regimes. All data other than percentages are based on the mean total plant production per treatment at the end of the experiment.

Species and Treatment	Plant wt (mg)	Nutrient content (%)			Total nutrients/ plant (mg)			mg nutrient accumulation/ mg root		
		N	P	K	N	P	K	N	P	K
<i>Arctagrostis latifolia</i>										
15°C, unfertilized	361.8	1.16	.18	2.49	4.27	0.66	9.17	19.84	3.08	42.60
8 to 0°C, unfertilized	182.5	1.24	.18	2.21	2.26	0.33	4.03	19.14	2.78	34.12
15°C, fertilized	785.4	1.16	.23	2.46	9.11	1.80	19.32	21.90	4.34	46.45
8 to 0°C, fertilized	405.0	1.42	.17	2.30	5.75	0.69	9.31	25.78	3.08	41.77
<i>Calamagrostis canadensis</i>										
15°C, unfertilized	345.0	1.12	.25	1.31	3.86	0.86	4.51	20.85	4.65	24.38
8 to 0°C, unfertilized	149.6	1.55	.16	1.37	2.32	0.24	2.05	32.47	3.35	28.70
15°C, fertilized	805.7	1.09	.17	1.44	8.78	1.37	11.60	25.60	3.99	33.82
8 to 0°C, fertilized	287.1	2.02	.21	1.65	5.80	0.60	4.73	44.88	4.66	36.65

Percent phosphorus content was essentially the same for both species and though there was no consistent response to soil temperature, there was a trend toward a decrease in content at the lower soil temperatures. Cold soils decreased phosphorus uptake 50 to 70%, the largest decrease occurring for *Calamagrostis* plants grown in cold nutrient poor soils. However, per mg of root, phosphorus accumulation was larger for *Calamagrostis* in all cases except in warm, fertilized soils.

Potassium tissue content was 40 to 80% higher in *Arctagrostis* than *Calamagrostis*. Although for both species reductions of 50% or more occurred under cold soil conditions, potassium per plant was nearly twice as high in *Arctagrostis* as in *Calamagrostis* under all treatments. Potassium uptake per mg of root for *Arctagrostis* was higher for all treatments, the greatest differences occurring in warm soils.

Summary and Discussion

The laboratory studies show that both low soil temperature and low fertility result in significant reductions in plant production. When tested separately, each resulted in 50% reduction in plant growth, their combined effect reducing growth to only 15% of that occurring on warm, high nutrient soils. The addition of nutrients to cold arctic soils restored both root and shoot production to near the same level as that on warm soils. Morphologically, the effects of soil temperature and nutrients were expressed as differences in leaf length and tiller development, soil fertility having a greater effect on leaf length

while soil temperature was more influential on tiller development. Though shoot systems of both species were not significantly different in size under any treatment, the root system of *Arctagrostis* was consistently larger than that of *Calamagrostis* being reduced less by low soil temperature and responding more positively to nutrient additions at low temperatures. This was further expressed in root:shoot ratios, which, for *Arctagrostis* were consistently greater than one, while those of *Calamagrostis* were near unity or less than one.

Tissue nutrient analyses revealed that although low soil temperature leads to an increase in nitrogen on a percent basis, there is a 35 to 50% decrease in accumulation of both N and K on a weight basis. Phosphorus accumulation was cut by 50 to 70% in cold soils, the largest decreases occurring in *Calamagrostis*. Although the absolute amounts of nitrogen and phosphorus absorbed were nearly equal for both species, *Calamagrostis* had the greater accumulation per unit of root biomass. *Arctagrostis* absorbed nearly twice the potassium of *Calamagrostis* and had the greater efficiency of accumulation for this element under all treatment conditions.

Tissue water potentials of neither species were greatly affected by low soil temperatures, remaining relatively low in both warm and cold soils. *Calamagrostis* had consistently lower water potentials than *Arctagrostis*. The only statistically significant change due to treatment occurred in *Arctagrostis*, and represented a mean three bar decrease due to low soil temperature, and a three to four bar increase in response to increases in soil fertility.

Net assimilation rates of both arctic species remained positive at even very low light intensities, the compensation point occurring at intensities below 40 lux. This agrees with the results for *Carex aquatilis* at Point Barrow (Tieszen, 1972) and *Carex stans* at Devon Island (Mayo *et al.*, 1974), both species having compensation points in the vicinity of 0.01 ly/min. This is in contrast to northern prairie grasses, which even under light intensities as high as 60,000 lux and at soil temperatures of 30°C, have fixation rates 20 to 30% lower than arctic grasses growing at one tenth the light intensity and at soil temperatures of 8°C (Redmann, 1970). At intensities of under 10,000 lux the fixation rate of prairie grasses drops off quickly, going to zero between 2,000 and 5,000 lux, while both arctic grasses maintain a positive assimilation rate down to 40 lux. Though some of the difference may be accounted for by the fact that Redmann ran his analyses on entire plants while in this study analyses were run on only a single leaf, the general trend is probably still valid. Only *Arctagrostis* was tested over a range of soil temperatures. Net assimilation dropped 25% with a reduction in soil temperature from 12°C to 4°C.

The data suggest that neither light intensity or low temperature effects on water potential and net assimilation rates are the primary reasons for the generally low growth rates under natural conditions. The relatively high rate of assimilation at low light intensities suggests that both species are able to make maximum use of 24 hr daylength conditions during the summer, continuing to fix energy

at low sun angles or during periods of coastal fog. The positive net assimilation rate at low soil temperatures, coupled with a relatively low tissue water potential, suggests that stomates remain open even though the plant remains under a continuous relative stress. This phenomena has been noted in other arctic species and has led some authors to suggest that the maintenance of this stress even under warm high moisture conditions may be an adaptation to prevent frost injury (Courtin and Mayo, 1973).

In this study it has been shown that low soil temperatures acting directly on root systems result in significant reductions in plant growth, even under optimum air temperatures, light intensities, soil moisture and nutrients. The exact mechanism is still not known, but the data suggest that low soil temperature can reduce the ability of these grasses to accumulate certain nutrients by 50 to 70% and that the addition of nutrients to a cold soil can stimulate growth to equal that of a warm soil. Though nutrients are shown to be low in the soils gathered from Tuktoyaktuk, the present study suggests that it is low soil temperature acting to further restrict the supply of nutrients to the plant which results in the generally low growth encountered in areas underlain by permafrost.

Though both species tested take up nearly equal amounts of nitrogen and phosphorus, they achieve this in different ways. *Calamagrostis* has a root system which is more restricted by low soil temperatures than that of *Arctagrostis*, but in terms of nutrient accumulation

per unit of root biomass, it is more efficient. The root system of *Arctagrostis*, though less efficient, is less restricted by low soil temperatures, compensating for a reduced efficiency by producing a greater root mass. The reason for the increased efficiency in *Calamagrostis* is not known but it is not believed to relate so much to specialized enzymes as to a greatly increased absorbing surface area due to a much finer root system.

These differences in root systems may help to explain the differences in range and habitat preference of these species. *Arctagrostis*, with a reduced efficiency but ability to produce a greater root mass at low soil temperatures, is at a competitive disadvantage in warmer surface horizons where most root systems are located, and is restricted to areas with deeper active layers occupied by fewer roots. In addition it has been observed that *Arctagrostis* tends to favor areas of mineral versus peat soil which may be due to the greater bulk density improving the root:soil contact. *Calamagrostis*, with its finer but more efficient root system, though restricted by low soil temperatures, has a root system better adapted to compete for nutrients in the warmer surface organic horizons. However, this species is of temperate origin, and in the Tuktoyaktuk Peninsula it is at its northern limit of range. The combination of low soil temperature reducing the root systems and limiting its area of nutrient extraction, and the increasing competition with other tundra species possibly better adapted to existing under low nutrient regimes, results in a species of very low vigor.

Both species are able to take advantage of previously untapped nutrient reservoirs which are exposed in deeper active layers following disturbance. The environmental and physiological factors believed to influence natural distribution and rapid colonization of disturbed areas by these species will be summarized and discussed in the following chapters.

Chapter VIII

INTEGRATION

In the preceding chapters various aspects of the ecology of *Arctagrostis* and *Calamagrostis* species have been described and discussed. The objective of this section is to integrate these factors where possible into an explanation of the role and importance of these species in disturbed and undisturbed tundra habitats.

Of the many factors affecting the ecology of *Arctagrostis* and *Calamagrostis*, the natural or accelerated man induced disturbance of tundra communities is one of the most important. In the undisturbed hummocky low shrub-heath tundra of the Tuktoyaktuk Peninsula both species are common but minor components of many plant communities, seldom comprising more than 1% of the total cover. Neither species is very vigorous, producing small inconspicuous vegetative clumps which spread rhizomotously. Relatively few flowering heads are produced although *Arctagrostis* produces some heads wherever it occurs.

With disturbance, such as the removal of the entire vegetative mat as occurred with the 1965 seismic lines, large changes took place in the vigor and cover of these species. In many disturbed habitats cover of both species increased thirty to seventy fold and they frequently make up 30 to 80% of the total vascular plant cover. Flowering, seed production and vegetative growth increased sharply, with net annual above ground production of these two species alone being four to five times greater than that of the adjacent undisturbed communities.

Field data suggest that of the microenvironmental changes related to disturbance the removal of the turf and the concomitant increase in soil temperature (Table 5) and active layer depth (Table 7) are the most influential in stimulating these growth changes. Air temperature is little affected by the removal of vegetation, temperature within the vegetation seldom being more than 1 to 2°C warmer than ambient air. Nutrient contents of disturbed and undisturbed soils are low and essentially the same, though undisturbed soils have a high organic volume while disturbed soils are primarily mineral. Soil moisture is seldom limiting in any tundra habitat (Table 9). Gravimetric measurements of soil moisture show that while surface soils may occasionally dry to 15 bars, subsurface soil moisture is seldom below 3 bars.

Both soil temperature and active layer depth increase significantly with disturbance. The greatest increases occur between disturbed areas and adjacent undisturbed hollows, mean active layer increasing 30 to 40 cm and soil temperature 8 to 10°C. Hummocks, because of their conical shape which improves drainage and maximizes energy reception, are more similar to disturbed areas, disturbance resulting in only a 10 to 20 cm increase in active layer and a 3 to 4°C increase in soil temperature. It is on these hummocks where these grasses most frequently occur in the undisturbed tundra.

These changes in microenvironment influence two important stages of a plant's life cycle: 1) seedling establishment (invasion) and 2) growth and development (colonization). Both entail a biotic response

to disturbance. Though many species in the tundra have the potential to respond positively in one or the other of these areas only those which can do so in both will successfully monopolize a new area.

Biotic Response To Disturbance

Germination and Establishment

The removal of all turf down to mineral soil provides an opening in an essentially closed tundra community for seedlings to establish. However for this to occur viable seeds must be produced which can reach and germinate in the disturbed habitat. All of the important cover species in the undisturbed tundra produce seed, many of which easily reach disturbed areas in quantity. Studies revealed that seeds of many of these plants (ie. *Betula nana* ssp. *exilis*, *Carex Bigelowii*, *Lupinus arcticus*) have low viability or do not germinate easily (Table 13). For other species, such as *Eriophorum vaginatum*, initial viability is high but seed production does not correspond to a favorable period for germination. Seed of this species requires temperatures of 20°C or warmer for germination. However, when produced near mid-July, though disturbed surfaces are warm enough, most are too dry for germination. In addition viability drops off sharply over only a three month period (Wein and Maclean, 1973) further reducing the chances for seedling establishment.

Though of low cover importance in the undisturbed tundra, *Arctagrostis* and *Calamagrostis* produce a small but mobile and highly viable

seed supply. Seeds of both species are very light (4500 to 5000 seeds/g) and may easily be wind borne, especially those of *Calamagrostis* which have a fluff of hairs around the callus. Seed maturity occurs late in the growing season just before freeze up when environmental conditions are unfavorable for germination. Field studies reveal that these seeds, either remaining in the head or lying on the soil surface, remain viable over winter and in a condition to germinate in the early spring. The seeds of both species germinate at temperatures as low as 5°C but require a moist surface (Table 14). The added snow caught in seismic lines and other disturbances due to permafrost subsidence keeps surface soils moist for a longer period of time enabling seeds to germinate and begin to establish. However by mid to late June, surface soils of most upland areas are too dry for seed germination. For those species able to germinate and produce a root system, disturbed subsurface soils remain moist enough throughout most of the growing season to provide ample moisture for growth and development.

Growth and Development

Although invasion is purely a chance event, dependent upon the arrival of the seed in a suitable microhabitat, once the seedling is established the colonization of disturbed areas is a function of the increased active layer and the growth, spreading ability and vigorous seed production of these two species. The first one to two years of growth of both of these grasses is slow and even in disturbed areas the small clumps (3 to 5 cm dia.) are inconspicuous. After this establishment period they grow rapidly and flower and fruit vigorously; net

above ground production of these two species alone being five times greater than that of the adjacent undisturbed tundra and flower and seed production increasing three to five times.

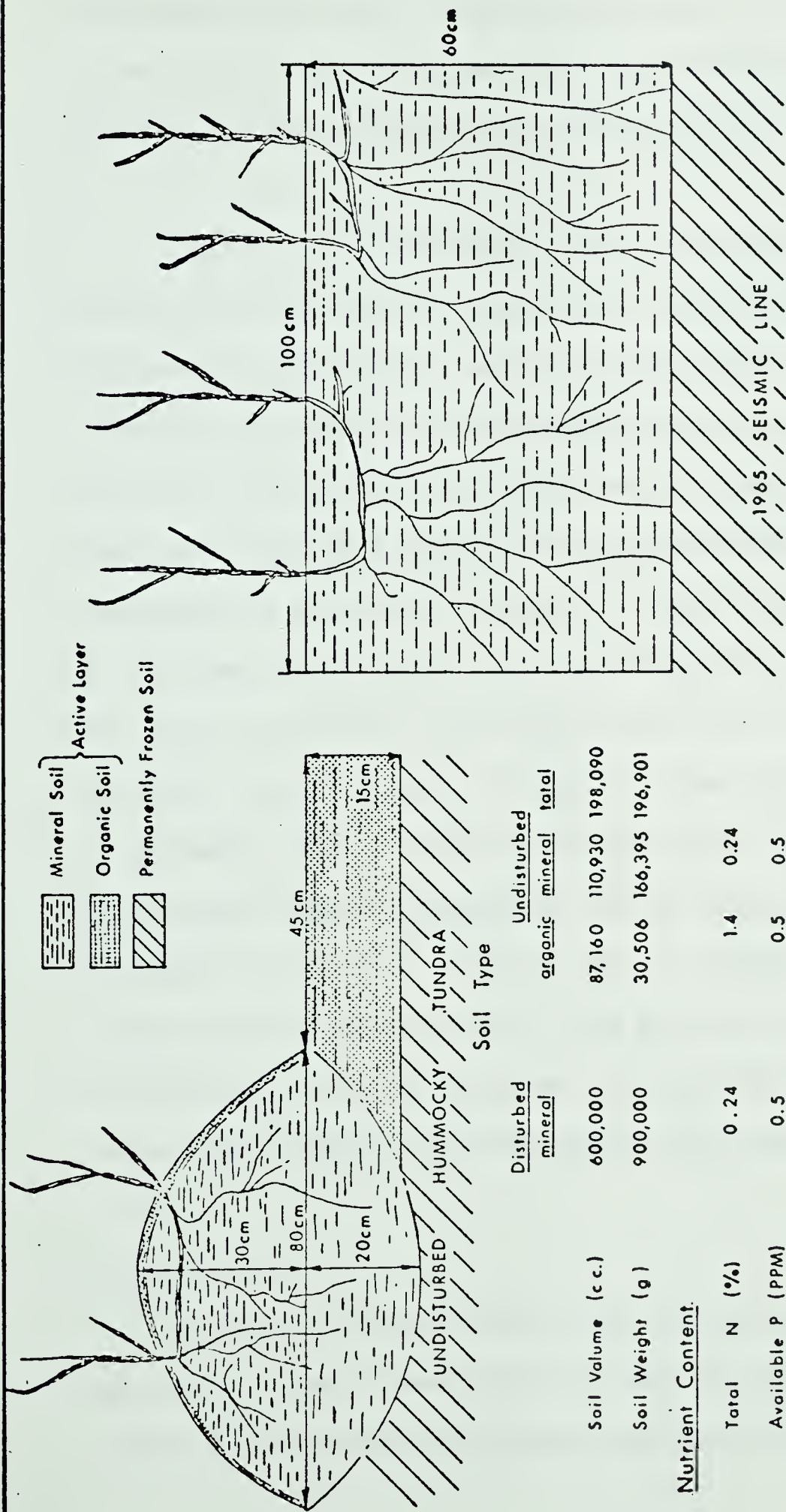
Though plants are larger and more vigorous in all disturbed locations, the tallest individuals, the highest percentage of flowering and the highest seed production are found in the disturbed mid-slope position. This position because of its inclination to the sun also has the deepest active layer and warmest soil temperatures. A comparison of plant heights and active layer depths in both disturbed and undisturbed areas showed a strong positive correlation between the two. Field data suggest that the increased size and vigor associated with warmer soils and deeper active layers is a result of an increased nutrient supply. Tissue nutrient contents (Table 12) of nitrogen and phosphorus are 50 and 75% higher respectively in plants growing in disturbed areas having a mean active layer depth of 60 cm vs. plants growing in undisturbed areas with a mean active layer depth of 36 cm. Janz (1974) studying plant and soil relationships on undisturbed sites on the Tuktoyaktuk Peninsula found a similar relationship between active layer depth and tissue nutrient contents, an increase in active layer depths between hill-tops and depression of 7 cm leading to 14% increases in both nitrogen and phosphorus tissue contents. Although further research is needed, it is interesting to note that in both studies there was an approximate 2 to 3% increase in tissue nitrogen and phosphorus with each centimeter increase in active layer.

Nutrient Pool

When expressed on a weight basis there is little difference in the total nitrogen or available phosphorus and potassium found in either disturbed or undisturbed soils. However the large increases in active layer after disturbance result in large increases in the soil volume available for root exploration and nutrient extraction. Jenny *et al.*, (1950) observed this same relationship in terms of soil volume to bedrock in temperate regions and Heilman (1968), working in forested permafrost regions, has expressed nutrient reserves based upon the volume of soil to the permafrost table. Figure 10 diagrammatically represents a cross section through the hummocky undisturbed tundra and the adjacent 1965 seismic line. The volume calculations are based upon mean active layer depth of the disturbed and undisturbed hill-top position and equal areas of one square meter. The hummock is 80 cm across, 30 cm high and has a maximum active layer of 50 cm. Hummocks generally consist of mineral soil, having only a thin organic layer (5 cm) over the surface and are separated from other hummocks by hollows or depressional areas. These areas have shallow active layers which are primarily organic matter. In the figure it is represented as having an active layer depth of 15 cm, width of 45 cm and length of 80 cm. Figuratively speaking each hummock is an island of relatively deep, warm mineral soil surrounded by a sea of ice.

To facilitate calculations of volume, a hummock was considered to consist of above and below ground spherical segments having a common base of 80 cm and heights of 30 and 20 cm respectively. Soil masses

Figure 10. Longitudinal sections through the active layers of equivalent (m^3) portions of undisturbed hummocky tundra and 1965 seismic line comparing volume, mass and nutrient contents of the soils.



within the active layer are based upon bulk densities of 1.5 and .35 for mineral and organic soils respectively. Nutrient determinations of undisturbed soils by Janz (1974) and of disturbed soils from this study were used in calculating total nutrients.

As can be seen from Figure 10, total volume of soil for root exploration is tripled by disturbance. More importantly, this volume represents a 2.5 fold increase in total nitrogen, a 2 fold increase in available P and a 4 fold increase in available K. When one considers, in addition, that disturbance removes all competition and that the disturbed areas in a seismic line are considerably larger than that portrayed, it can be seen that plants able to quickly reach and establish in this area have access to a large untapped nutrient pool. However, the depth and volume on the active layer is not the whole key to the increased nutrient supply. Though unfrozen, the active layer even in disturbed areas is still a cold medium for root growth, restricting the size and depth of penetration of the absorbing organ. Both field and laboratory evidence suggests that in addition to the absolute increase in the nutrient pool, it is the tolerance of *Arctagrostis* and *Calamagrostis* roots to growth in cold soils which enables them to more fully exploit the increased active layer.

Cold Tolerance

Studies by Bliss (1956) of the rooting habits of tundra species near Umiat, Alaska showed that the root and rhizome systems of most shrubby and Ericaceous plants were restricted to the upper 3 to 7 cm

of the organic soil. He reported that grasses and sedges were the types of plants which most frequently sent roots deep into the active layer and cited observation of *Arctagrostis* roots growing within several centimeters of the retreating frost table. Experimental evidence confirms this as roots of both *Arctagrostis* and *Calamagrostis* were shown to possess the ability to grow into and extract nutrients from soil zones as cold as 2°C. *Arctagrostis* was the better adapted of the two, the size of its root system being unaffected by temperatures between 8 and 5°C while that of *Calamagrostis* was reduced by 40% (Table 21). However *Calamagrostis* has a more finely branched root system and partially compensates for this size reduction with an apparently more efficient uptake, accumulating nearly the same amounts of nitrogen and phosphorus as did *Arctagrostis* (Table 24).

Growth In Undisturbed Habitats

This experimental evidence also suggested reasons for the observed distribution and vigor of these species in undisturbed habitats. *Arctagrostis* is most important in areas having an active layer deeper than 30 cm such as hummocks, while *Calamagrostis*, though lacking in vigor in all habitats, tolerates a wider range of habitats many of which have shallow active layers. For a plant such as *Arctagrostis*, able to tolerate low soil temperatures but possibly lacking the efficiency to compete for nutrients in the warmer organic layer, the hummock represents a small but relatively exclusive volume of mineral soil. However competition by other species in the warmer horizons and the

limitation on the size of the mineral area by the surrounding frozen hollows, limits both vigor and further expansion of this species. For *Calamagrostis* the situation is somewhat different. It has a more finely branched and more efficient root system. However the size of its root system is much more reduced by low soil temperature than that of *Arctagrostis* often restricting the species to the shallower and somewhat warmer organic layer where it is in competition with many other species. The fact that it is a boreal species at the northern limits of its range, coupled with the increased competition with other species possibly better adapted to slower growth rates and/or low nutrient supplies, results in the observed generally low vigor.

Role In The Tundra

The large increases in net above ground production as a result of disturbance and the laboratory studies of growth in cold arctic soils suggest that, at least for the two grasses in question, low soil temperature acting to further limit an already limited nutrient supply is a major factor restricting growth in the undisturbed tundra.

Because the vigor and spreading ability of these grasses is limited in undisturbed tundra, their maintenance is dependent upon some form of disturbance which will enlarge their nutrient supply. In this sense they may be considered ecological opportunists, not well adapted to the closed tundra situation but having the ability to survive by producing viable seeds until some type of disturbance

provides a more suitable habitat. Once a disturbance occurs their viable and easily germinated seed, coupled with a comparatively rapid growth, enables them to quickly invade and colonize an area. The maintenance in natural communities of small but well adapted populations of colonizing species is one of nature's ways of repairing natural disturbance. The role of these grasses in the Arctic is similar to that of many successional species in temperate regions, their invasion and rapid growth tending to dampen fluctuations in the ecosystem by stabilizing soils and maintaining the flow of energy into and through the system. In a limited sense they may even lead to the nutrient enrichment of an area. The exposure of an untapped nutrient pool by an increase in active layer provides a source of added nutrients if they can be extracted from colder soil zones and brought to the surface. *Calamagrostis* and especially *Arctagrostis* appear to serve in this function by sending roots deep into these zones. Whether or not of major ecological importance, their high production on disturbed sites results in a rapid accumulation of a nutrient rich biomass which gradually increases the nutrient status of the disturbed area.

Although the successional sequence is not known it is expected that with time the accumulation of litter and an increase in plant cover will cool the soils and allow the permafrost table to rise. The reduction of the nutrient supply as the soil volume is reduced and the increased competition as shrubby species begins to reinvade these areas is expected to gradually limit the expansion of these grasses and lower their vigor. Eventually the former tundra communities are expected to re-establish.

Chapter IX

SUMMARY

A comparative study was made of the ecology of *Arctagrostis latifolia* and *Calamagrostis canadensis* to determine the factors influencing their distribution and importance in disturbed and undisturbed tundra communities on the Tuktoyaktuk Peninsula, N.W.T. This included documentation of their range and taxonomy and studies of: 1) their occurrence and importance in tundra communities, 2) microenvironmental changes related to disturbance, 3) growth and phenological response to disturbance, 4) seed germination, and 5) growth in cold soils.

Range and Taxonomy

1. *Arctagrostis latifolia* has a circumpolar distribution and a north-south range between 55 and 85⁰. The genus consists of only two to three distinct species, members of which are believed to have migrated to North America from the mountains of northeast Asia prior to the last glacial period. Trapped in refugia north of the advancing Pleistocene glaciers, they evolved in comparative isolation.

2. *Calamagrostis canadensis* is an arctic-boreal species limited to the North American continent but having a N-S range between 35 and 70⁰. The genus contains over 100 species, many of which occurred south of the advancing ice sheet. *Calamagrostis canadensis* is believed

to have arisen from this diversified gene pool with a relatively wide ecological amplitude.

Occurrence and Importance in Tundra Habitats

3. Field studies were conducted on the Tuktoyaktuk Peninsula located on the Arctic Coastal Plain to the east of the mouth of the Mackenzie River. The topography is gently rolling with a relief of less than 45 m. Permafrost is continuous and frost features such as hummocks, polygons and pingos are common. Thirty to 50% of the region is covered by lakes, many of which are of thermokarst origin.

4. Soil and vegetation patterns have developed in response to variations in soil moisture influenced by permafrost and topography. These range from associations of Gleysolic and Regosolic Turbic Cryosols and dwarf shrub-heath vegetation on imperfectly drained hill-tops to Mesic Organo Cryosols and sedge meadows in wet lowland.

5. *Calamagrostis* is found in a variety of undisturbed tundra habitats from those having shallow and imperfectly drained active layers to those which are deep and moderately well-drained. In no undisturbed habitat is it very vigorous, generally existing as small clumps of weak, chlorotic leaves and seldom producing flowering stalks.

6. *Arctagrostis* is found in fewer undisturbed habitats, being most important in those having imperfectly drained soils and an active layer greater than 35 cm. In all areas of occurrence it produces seed heads.

7. Both grasses are important colonizers of disturbed habitats except for those which are very wet, their cover increasing 30 to 80 times above that in the adjacent undisturbed tundra. Important species in the undisturbed tundra such as *Betula nana* ssp. *exilis*, *Salix glauca*, *Eriophorum vaginatum*, *Vaccinium vitis-idaea* ssp. *minis* and *Lupinus arcticus* are much slower invaders of disturbed sites and seldom produce cover as high as that of either grass.

Microenvironment

8. Studies of microenvironmental changes related to disturbance were conducted along a northeast-facing hillside in a 1965 seismic line and adjacent undisturbed tundra. Measurements included active layer depths, air, surface and soil temperatures, soil nutrients and soil moisture.

9. Much of the upland tundra is hummocky, consisting of small conical mounds 20 to 30 cm high and 50 to 100 cm in diameter, separated by smaller depressional areas 30 to 40 cm across. The hummocks, often containing a mineral soil core, are warmer and somewhat drier than the hollows having in mid-July a mean temperature at -10 cm of 7.5°C

vs. 1.5°C for hollows and an active layer of 40 to 50 cm vs. 15 to 20 cm for hollows.

10. Summer seismic lines of the mid 1960's led to the removal of all vegetation and soil down to permafrost (20 to 30 cm). Following permafrost melt the ground surface subsided another 20 to 30 cm, resulting in a surface 50 to 60 cm below the surface of the adjacent tundra. In mid-July, soil temperatures at -10 cm are 10 to 12°C and active layers 50 to 60 cm. Disturbed mid-slope positions are 1 to 2°C warmer and have active layers 15 to 20 cm larger than disturbed top or bottom slope positions.

11. In spring the depression formed by disturbance is snow filled one to two weeks longer than undisturbed areas. Disturbance has little effect on available soil moisture, most soils remaining moist throughout the growing season except for disturbed surface soils which tend to reach the permanent wilting point more frequently.

12. Nutrient status of disturbed and undisturbed soils are little different. The nutrient rich organic mat is removed but its removal is more than compensated for by large increases in the active layer depth and thus the available nutrient reservoir.

Plant Response to Disturbance

13. Response of the two grasses to disturbance was measured

in terms of growth, vigor and phenology. Disturbance resulted in 15 to 50 more shoots per clone, 3 to 5 times more flowering heads, up to 5 times more seeds per head and increases in plant height from 65 to 165%. The net annual above ground production of the two grasses in the disturbed area was 280g/m^2 , five times that of the adjacent undisturbed tundra. The largest absolute values for most of these factors occurred at the disturbed mid-slope positions.

14. Phenology is unaffected by either disturbance or slope position, however, the development of *Arctagrostis* is in advance of that of *Calamagrostis*, having seed set by the middle of August while *Calamagrostis* is just beginning anthesis.

15. Plants growing in disturbed areas have significantly higher tissue concentrations of nitrogen and phosphorus and are under a somewhat lower tissue water stress.

16. *Arctagrostis* is the larger and more vigorous of the two grasses, producing 2 to 3 times as many flowering heads, 50 to 150 times as much seed and 80% of the total net production of these two species in disturbed areas.

Seed Germination

17. Germination tests of a number of arctic species revealed that the seeds of colonizing species, though providing a much lower

total seed source, are more viable and/or more easily germinated than non-colonizing species.

18. Seed from both grasses were highly viable having germination percentages at room temperature ranging from 80 to 95%. Of the two, *Arctagrostis* has the highest rate and most complete germination at temperatures below 20°C with an abrupt germination cutoff above 30°C while for *Calamagrostis* the highest rates and percent germination were above 20°C with little reduction in germination of temperatures up to 35°C. Germination of both species was greatly reduced by a -6 bar water stress.

19. Both disturbance and slope position have significant effects on the germination of *Arctagrostis*, the speed and completeness of germination being greater in collections from disturbed than undisturbed sites. Collections from the disturbed hilltop and mid-slope positions have faster and more complete germination than those from the hill bottom position.

Plant Growth in Cold Soils

20. Plants of both species were grown in growth chambers under varying conditions of soil temperature and nutrients for eight weeks while light, air temperature and soil moisture were kept near optimum. Measurements were made of root and shoot production, leaf water potentials, nutrient accumulation and CO₂ exchange.

21. Both low soil temperature and low soil fertility reduced plant production by 50 to 60%, their combined effects reducing growth by 85%. The addition of nutrients to cold arctic soils restored root and shoot production to near the same level as that on warm soils.

22. The shoot systems of both species responded similarly to all treatments, however the root system of *Arctagrostis* was much less reduced by low soil temperatures and responded more positively to nutrient additions at low soil temperatures. Root:shoot ratio of *Arctagrostis* was consistently greater than one while that of *Calamagrostis* was one or less than one. On cold, low nutrient soils, *Arctagrostis* produced nearly twice the root system of *Calamagrostis*.

23. Total nutrient accumulation for both species was reduced 35 to 50% for nitrogen and potassium and 50 to 70% for phosphorus at low soil temperatures. Under all treatments *Calamagrostis* had the greatest accumulation per unit of root biomass for nitrogen and phosphorus while *Arctagrostis* was more efficient in the accumulation of potassium.

24. Tissue water potentials of both species were little effected by low soil temperatures. Values remained low even though soils were maintained at field capacity. However in warm soils *Arctagrostis* responded to the addition of nutrients with a significantly more positive water potential.

25. Leaves of both species maintained high net assimilation rates at low light intensities, maintaining a positive net assimilation rate at intensities as low as -40 lux. *Arctagrostis* net assimilation was measured at soil temperatures from 15 to 3°C. Assimilation did not decline significantly until a temperature of 4°C was reached and then was reduced 25% below the maximum occurring at 15°C.

On the basis of this study it is believed that low nutrient availability, a function of nutrient deficient soils, shallow active layers and competition from other species, is one of the major factors limiting the growth of these grasses in the undisturbed tundra. Neither grass appears to be well adapted to competition for nutrients in the upper, warmer soil horizon where most roots are concentrated. Instead they depend upon areas of deep soils and a root tolerance to low soil temperatures to provide them with a limited but relatively exclusive volume of soil for nutrient extraction. *Arctagrostis*, having the more cold tolerant but less efficient root system of the two, is more restricted in its distribution, occurring primarily in areas of deeper thaw. The greater efficiency of nutrient accumulation of *Calamagrostis* enables it to compete with other species in shallower soils, expanding the number of habitats in which it can be found. However, the fact that it is at the northern limits of its range and that its root system is more restricted by low soil temperature than that of *Arctagrostis*, results in a large reduction in vigor.

Surficial disturbance as occurs with the removal of the vegetation and insulating organic mat creates an opening in an otherwise closed tundra community and results in a warming of the soil and the concomitant increase in the volume of the soil and the size of the nutrient pool. *Arctagrostis* and *Calamagrostis*, though of low cover importance in the undisturbed tundra produce a small but mobile and highly viable seed supply. Unlike many tundra species, the seed of these grasses germinate over a wide range of temperatures and require no special pretreatment. Once established, the production of root and rhizome systems which are tolerant of low soil temperature aids in the exploration and utilization of the newly expanded volume of soil. This rapid growth and rhyiomatous spreading ability, coupled with a vigorous seed production results in a relatively rapid colonization of disturbed areas. In time, their rapid biomass production is expected to insulate the soils enough to allow the permafrost table to rise, reducing the size of their nutrient pool and providing a more suitable habitat for deciduous and evergreen shrubs and associated forbs.

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